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Competitive learning modulates memory consolidation during sleep

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ABSTRACT

Competition between memories can cause weakening of those memories. Here we investigated memory competition during sleep in human participants by presenting auditory cues that had been linked to two distinct picture-location pairs during wake. We manipulated competition during learning by requiring participants to rehearse picture-location pairs associated with the same sound either competitively (choosing to rehearse one over the other, leading to greater competition) or separately; we hypothesized that greater competition during learning would lead to greater competition when memories were cued during sleep. With separate-pair learning, we found that cueing benefited spatial retention. With competitive-pair learning, no benefit of cueing was observed on retention, but cueing impaired retention of well-learned pairs (where we expected strong competition). During sleep, post-cue beta power (16–30 Hz) indexed competition and predicted forgetting, whereas sigma power (11–16 Hz) predicted subsequent retention. Taken together, these findings show that competition between memories during learning can modulate how they are consolidated during sleep.

1. Introduction

Memories do not exist in a vacuum. Rather, each memory exists in a network with related memories that compete at retrieval with the sought-after memory. Prior studies have found that competition can lead to weakening of competing memories (Anderson, Bjork, & Bjork, 2000; Kim, Lewis-Peacock, Norman, & Turk-Browne, 2014; Lewis-Peacock and Norman, 2014; Newman and Norman, 2010; Norman, Newman, & Detre, 2007). These modifications adaptively shape the memory landscape, reducing the degree of competition on subsequent retrieval attempts (Norman et al., 2007).

Although these studies of memory competition have focused on retrieval during wake, similar competitive dynamics could occur during sleep. We know very little about how memories interact during sleep, given that studies of memory reactivation during sleep have focused on the retrieval of isolated memories, with a few notable exceptions (Genzel et al., 2017; Oyarzún, Moris, Luque, Diego-Balaguer, & Fuentemilla, 2017; Payne, Stickgold, Swanberg, & Kensinger, 2008).

To gain empirical leverage on memory competition during sleep, we used a technique called targeted memory reactivation (TMR; Oudiette and Paller, 2013). TMR involves biasing reactivation by presenting learning-related stimuli during sleep (Bendor and Wilson, 2012). Prior studies have found that TMR of isolated memories is beneficial for those memories (Oudiette, Antony, Creery, & Paller, 2013; Rudoy, Voss, Westerberg, & Paller, 2009; Schreiner, Lehmann & Rasch, 2015); in this study, we explored what happens when we present TMR cues that have been linked (during wake) with multiple learning experiences. Participants (n = 60; Fig. 1) first learned arbitrary associations between specific environmental sounds and pictures. Some sounds were linked with two pictures from different categories (paired), whereas other sounds were linked with one picture (singular). Participants then learned the location of each picture against a background grid, as well as the reward that would be provided if they remembered the picture's location; for paired pictures, one picture was assigned a high reward and the other a low reward. Next, memory for picture-location associations was tested, followed by a nap. Sound cues (100% of singular and 50% of paired sounds) were presented to the participants during slow-wave sleep. After the nap, participants took a final picture-location test and sound-picture association test.

We hypothesized that placing paired memories into direct competition during wake, by asking participants to prioritize one memory over the other (Mather & Sutherland, 2011), would engender competition between these memories when they were cued during sleep. If so, one consequence predicted by the foregoing account would be memory weakening. We varied competition during wake by having participants learn the locations of pictures paired with a common sound cue either in a competitive-pair learning condition (CPL; n = 30) or a separate-pair learning condition (SPL; n = 30). For the CPL condition,

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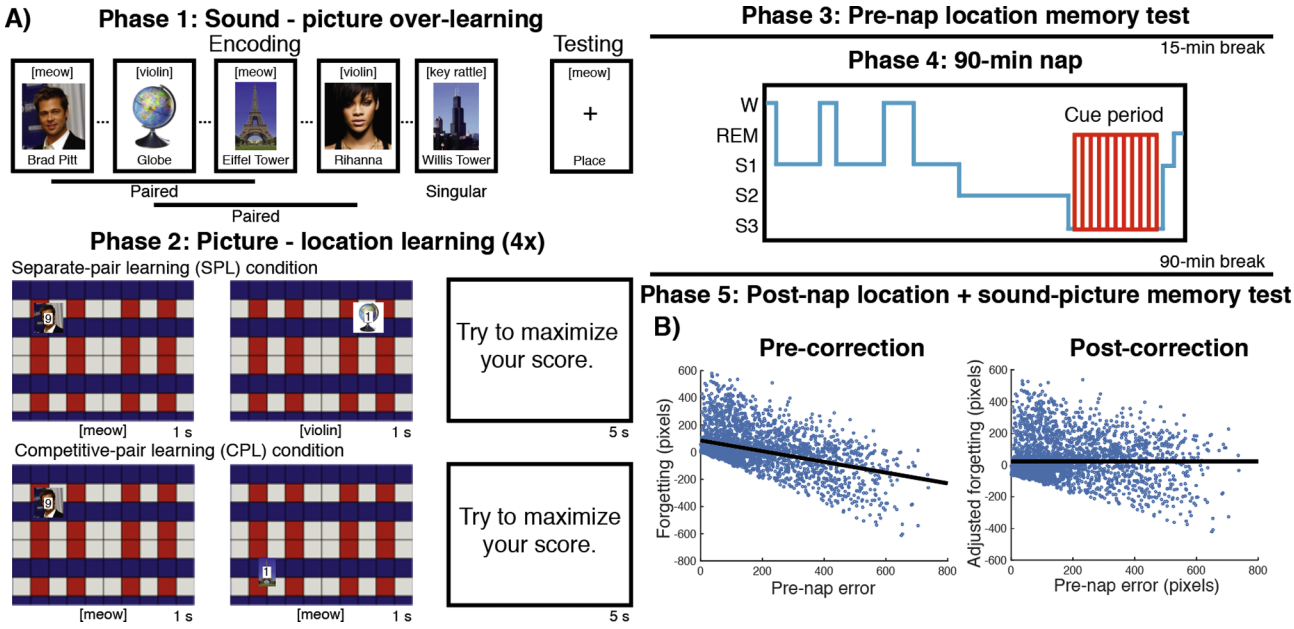

Fig. 1. Task design. (A) In phase 1, participants over-learned associations between sounds and pictures. Associations were tested by presenting the sound and the category of the picture until each association was correctly retrieved twice. In phase 2, participants encoded locations for the same pictures (along with their accompanying sounds) against a background grid. Each paired picture was assigned a high or low reward to be given upon correct recall, and each singular picture was assigned a high reward. The numbers depicting reward are enlarged here for expository purposes and did not obscure the picture in the actual experiment. Paired pictures were shown in groups of two for 1 s each before a 5-s period when participants were to prioritize rehearsal to maximize their score. Under separate-pair learning conditions (SPL), both pictures within a group were associated with different sounds, whereas under competitive-pair learning conditions (CPL), they were associated with the same sound. Singular pictures were shown alone before a similar 5-s prioritized recall period. In phase 3, participants took a test on each location. In phase 4, sounds from all singular and half of the paired pictures were presented during SWS. In phase 5, participants took a final test on each location followed by a sound-picture test on the associations formed during phase 1. (B) Demonstration of the forgetting metric. (left) Pre-nap spatial error significantly predicts forgetting (post – pre-nap spatial error). (right) Adjusted (residual) forgetting values after regressing out pre-nap spatial error and adding mean forgetting.

competition was maximized because participants studied the locations of paired pictures in direct succession, followed by a 5-second rehearsal period in which they were told to "maximize their score" (presumably by rehearsing the location of the high-reward picture in the pair; Oudiette et al., 2013). Thus, in this condition, participants were guided to directly prioritize one picture location in a pair over the other. In the SPL condition, the locations of paired pictures were not studied in succession and participants were never asked to prioritize one paired picture location over its direct competitor, thereby reducing competition within the pair.

In short, we predicted that competition during learning would interact with TMR effects, such that TMR cues would benefit memory in the SPL condition but would show less of a benefit (due to competition-based weakening) in the CPL condition. We also predicted a three-way interaction between learning condition (SPL/CPL), cueing, and reward. Specifically, we predicted that TMR cues would benefit spatial memory for non-competing pictures (SPL) at both levels of reward. However, we predicted that competing pictures (CPL) would show a "zero-sum" pattern: Based on prior work showing that reward prioritizes replay (Gruber, Ritchey, Wang, Doss, & Ranganath, 2016; Murty, Tompary, Adcock, & Davachi, 2017; Stickgold and Walker, 2013), we predicted that the high-reward picture would win the competition (benefiting spatial memory, or at least avoiding weakening) and the low-reward picture would lose the competition (weakening spatial memory for that picture). We also collected EEG data during sleep. Prior studies linked memory strengthening via TMR with post-cue sigma power (Lehmann, Schreiner, Seifritz, & Rasch, 2016; Schreiner, Lehmann et al., 2015) and memory weakening with post-cue beta power (Oyarzún, Moris, Luque, de Diego-Balaguer, & Fuentemilla, 2017). Accordingly, we hypothesized that the benefits and costs of TMR would be related to sigma and beta power, respectively. Our experiment thus aimed to shed light on both neurocognitive mechanisms and associated neurophysiological measures.

2. Materials and methods

2.1. Participants

Sixty participants (43 female, 18–35 years old) were recruited via online scheduling software at Princeton University (n = 37, 27 female) and Northwestern University (n = 23, 16 female). Data were collected in approximately similar proportions for the two conditions at the two universities (SPL: 18 Princeton, 12 Northwestern; CPL: 19 Princeton, 11 Northwestern). Forty other participants (17 Princeton, 23 Northwestern) were excluded for not sleeping long enough for at least one round of sleep cues. Participants were given hourly monetary compensation for participating and small additional increases based on good performance. This experiment comprised either a separate-pair learning (SPL) condition (n = 30, 22 female) or a competitive-pair learning (CPL) condition (n = 30, 21 female). Written informed consent was obtained in a manner approved by the Princeton and Northwestern University Institutional Review Boards.

2.2. Stimuli

We included 102 visual stimuli in equal proportions from three categories (celebrities, famous landmarks, common objects), updating the set used by Polyn et al. (2005). These pictures were associated with 66 unique sounds (e.g., "meow") lasting up to 500 ms adapted from those used by Oudiette et al. (2013). During the nap, sleep cues were embedded in constant white noise (~44 dB), resulting in increases of no greater than 5 dB.

2.3. Design and procedure

The experiment comprised five phases (Fig. 1). In phase 1,

participants over-learned arbitrary associations between sounds and pictures. The goal of this phase was to create strong associations that could consistently support sounds reactivating their corresponding associates during sleep. Thirty sounds were uniquely associated with a single picture (10 from each category), while the remaining 36 sounds were associated with two pictures from different categories. We will refer to pictures associated with a unique sound (not shared with other pictures) as *singular* pictures and pictures associated with the same sound as *paired* pictures. Sound-picture mappings were randomly shuffled for each participant. Sound-picture learning proceeded in four blocks of 20 and one block of 22 associations. Each self-initiated trial began with 1 s of a central fixation cross followed by auditory presentation of the sound and simultaneous visual presentation of the picture and sound label. The picture was shown centrally with the sound label above. Sound labels were included to eliminate ambiguity of sound identities and to facilitate learning. After 2 s, the sound was repeated and the picture label was included below the picture. After each picture had been studied once within a block, we tested participants' memory for sound-picture associations from that block. On each test trial, a sound was presented simultaneously with the corresponding sound label and a visual category name (e.g. "celebrity"); participants had to respond with the name of the picture from that category that had been linked to that sound. After participants responded, they were told the correct response. Each sound-picture association was tested until the corresponding picture name was correctly remembered, after which it dropped out. After all associations from a block were recalled, participants proceeded to the next block. After the fifth block, all associations were tested until participants retrieved each correctly again, so in total each association was correctly remembered twice.

In phase 2, participants learned arbitrary associations between pictures and locations against a background spatial grid. Pictures were presented in unique locations for 1 s each. Each picture was assigned either a high (9 cents) or low reward (1 cent); participants were informed that the reward would be provided at the end of the experiment if they correctly remembered the picture's location (< 150 pixel error). Each picture was shown with a height of 150 pixels (5.5 cm) centered around a random location between −300 and 300 pixels (−11.1 to 11.1 cm) from the center of the screen, with its reward value in the center of the picture (Fig. 1); the corresponding sound was also played during picture presentation, in order to reinforce associations learned in phase 1.

In the CPL (competitive-pair learning) condition, participants learned locations for paired pictures (i.e., pictures linked to the same sound) on successive trials. One picture in each pair was assigned a high reward, and the other picture in the pair was assigned a low reward. After the two paired pictures were presented in their (respective) locations, participants were given a 5-s rehearsal period where we instructed participants to maximize their score by freely rehearsing information in such a way as to give them the highest score. Given these instructions, we expected participants would selectively rehearse the high-reward picture-location association most often. Participants also learned locations for singular pictures (i.e., pictures associated with a sound that was *only* assigned to that picture). All singular pictures were assigned high rewards. After learning the location for a singular picture, participants were given a 5-s rehearsal period where they were encouraged to rehearse that picture-location association on its own.

The phase 2 procedure was the same for the SPL (separate-pair learning) condition, except for a crucial difference in how paired pictures were studied: In the SPL condition, the two consecutive pictures before a given rehearsal period were never linked with the same sound (in contrast to the CPL condition, when they were always linked with the same sound). In the SPL condition, the paired pictures that preceded each rehearsal period were randomly selected on each round, subject to the constraint that (before a given rehearsal period) the two pictures were associated with different sounds and also different (high vs. low) values. As such, under both SPL and CPL conditions, successive pictures appearing before a given rehearsal period always included one high- and one low-reward picture. Note that the instructions to rehearse the high-reward picture were identical in the two conditions, so the only difference between conditions was that participants were asked to prioritize one member of a same-sound pair over the other in the CPL but not the SPL condition.

In both the CPL and SPL conditions, participants viewed all picture-location pairings four times during phase 2, each time in a new, random order. We assigned equal distributions of each possible combination of category-A-high reward and category-B-low reward (e.g., celebrity-high reward + landmark-low reward). Participants were given breaks at intermittent intervals.

In phase 3, participants took a pre-nap test by dragging each picture from the center of the screen to its location. They indicated their spatial recall choice with a mouse click and were given no feedback. To-be-cued and to-be-uncued pairs were selected to equate pre-nap memory scores between these two conditions. Of the 36 pairs, there were 6 in each category X reward subcategory (e.g., there were 6 high-reward face, low-reward place pairs, 6 high-reward face, low-reward object pairs, etc.). Each set of 6 was pseudo-randomly scrambled into 3 cued and 3 uncued pairs, such that the 2 best pairs (calculating mean spatial error for both pictures of a pair) became one cued, one uncued, followed by the next two, and then the final two.

In phase 4, participants took an afternoon nap in the lab. Upon online indications of SWS (Rechtschaffen and Kales, 1968), we administered sleep cues once every 4.5 s unless they showed arousals. We cued all of the singular sounds and half of the paired sounds up to seven times. After 60 min, if participants had not received sounds, we administered them during indications of stage-2 sleep. After the nap, participants left the lab for 1.5 h.

In phase 5, participants returned to the lab to take a final spatial memory test followed by a final sound-picture test in the same manner as in previous phases. Following these tests, participants were debriefed and compensated for their participation.

Importantly, the purpose of singular pictures in our design was to allow us to assess EEG correlates of neural competition in response to TMR cues, by comparing EEG responses to singular-picture TMR cues (where we expected competition to be relatively low) vs. paired-picture TMR cues (where we expected competition to be relatively high). We also wanted to assess whether EEG correlates of subsequent spatial memory for paired-picture TMR cues resembled those obtained for singular-picture TMR cues. We allocated all singular pictures to the cued condition in order to maximize our power for looking at these physiological effects of cueing. Singular pictures were given high rewards to put singular-picture TMR cues on equal footing with paired-picture TMR cues – this way, both paired-picture and singular-picture TMR cues were linked to at least one high-reward picture.

2.4. Dependent variables

We used an adjusted spatial forgetting score as our primary dependent variable. Spatial forgetting, calculated as post-nap spatial error – pre-nap spatial error, significantly correlates with pre-nap spatial error. Pictures with highly accurate pre-nap spatial recall face ceiling effects (e.g. an error of only 2 pixels cannot be improved across the nap by more than 2 pixels) and those with poor pre-nap spatial accuracy follow a regression to the mean (e.g., an incorrectly recalled location, when very distant from the correct location, is likely to be recalled more accurately after the nap, even by chance). Therefore, we calculated the linear relationship between pre-nap spatial accuracy and forgetting (post-nap – pre-nap spatial accuracy) pooled across participants in the present data (Fig. 1B). Then we subtracted each spatial forgetting score from the spatial forgetting expected from this linear relationship (i.e., the residual) and, because this analysis zeros out forgetting, we added back the pooled mean raw spatial forgetting value to produce the adjusted spatial forgetting score used for all reported analyses (Antony

et al., 2018). We also calculated accuracy on the final sound-picture test; specifically, we calculated the proportion of correctly remembered pictures associated with cued and uncued sounds.

2.5. Experimental design and statistical analysis

Learning procedure (CPL vs. SPL) was manipulated between-participants. Picture type (singular, high-reward paired, low-reward paired) and TMR cueing (cued, uncued) were manipulated within participants, except that singular pictures were always cued. We selected a sample size of 60 (30 each in the CPL and SPL conditions) based on a slight increase in the sample size from a previous study of memory weakening during wake (n = 24; Kim et al., 2014). To assess the effects of CPL vs. SPL on initial spatial learning, we submitted pre-nap spatial errors to a mixed, 2 (condition: CPL vs. SPL) × 3 (picture type: singular, high-reward paired, or low-reward paired) ANOVA. To ask how competition condition, cue status, and reward status interacted for paired pictures, we submitted adjusted spatial forgetting measures for these factors to a mixed, three-way ANOVA. To ensure that differences in cueing effects between CPL and SPL were not due to differences in pre-nap learning, we subsampled the data to eliminate these pre-nap differences and reran the analyses; see *Permutation tests on pre-nap differences and condition interaction* below. To further probe how reward value and TMR interacted for paired pictures within the CPL and SPL conditions, we submitted memory retention measures to a 2 (reward: high vs. low) × 2 (cue status: cued vs. uncued) repeated measures ANOVA. All of these analyses included all participants. Statistical procedures assessing whether cueing effects were correlated within a pair are described in the *Paired forgetting interactions* section below. Statistical procedures assessing (within the CPL and SPL conditions) how pre-nap spatial accuracy interacted with TMR effects are described in the *Item* versus *competitor pre-nap accuracy bootstrapping procedure* section below. All of these analyses included all participants. To assess differences in sound-picture memory (on the final test) across conditions, we contrasted singular versus paired pictures using paired *t*-tests, and we ran 2 (reward: high vs. low) x 2 (cue status: cued vs. uncued) repeated measures ANOVAs to test the effects for paired pictures (separately within SPL and CPL).

Physiological analyses used bootstrapping procedures (described in the *Electrophysiological analyses* section) to identify time windows with significant differences. After relevant time windows were identified, we used ANOVAs to examine how different factors modulated oscillatory power in those time windows. For analyses predicting subsequent memory, participants without any trials in particular cells were dropped from the analysis.

2.6. Permutation tests on pre-nap differences and condition interaction

To ensure that differences in pre-nap spatial accuracy could not explain TMR differences between the two learning conditions, we randomly resampled 18–28 participants without replacement in both the CPL and SPL conditions, selecting 100 resampled instances in which the difference in high-reward pre-nap spatial accuracy between the groups was minimal ($t < 0.05$ for that instance). All trials within these subsets of participants were used. We chose a range of sample sizes randomly so the algorithm would not repeatedly choose the same sample of participants, then we calculated TMR effects for each of these selections. We also conducted resampling analyses collapsed across the CPL and SPL conditions to assess whether pre-nap differences could account for electrophysiological differences between various conditions (e.g., singular vs. paired; also, differences between subsequently remembered and forgotten items; see description of electrophysiological analyses below).

2.7. Paired forgetting interactions

A cueing benefit could mean that spatial memory for both pictures in a pair improves simultaneously, such that the two pictures have converging fates. Alternatively, cueing could be asymmetrically biased to improve spatial memory for one of two pictures, decreasing the likelihood of the other improving and creating diverging fates. Simply assessing overall trends for cued and uncued high- and low-reward pictures without specifically considering paired interactions cannot distinguish between these possibilities. To probe the relationship between paired pictures, we conducted median-split analyses on the adjusted spatial forgetting scores for both high- and low-reward pictures, creating four quadrants wherein picture pairs could fall (i.e., above-median-forgetting and below-median-forgetting, for both the high-reward picture and the low-reward picture). Next, we asked how many cued and uncued pairs fell within each quadrant. We simplified the analyses by considering the upper right quadrant to represent pairs in which adjusted spatial forgetting for neither picture was better than the median (*None Better*), the lower right and upper left quadrants to represent pairs in which adjusted spatial forgetting for one picture was better than the median *(One Better)*, and the lower left where adjusted spatial forgetting scores for both pictures were better than the median *(Both Better)*. Then, we calculated paired *t*-tests between the proportion of cued and uncued pictures in each bin (Fig. 3A). Intuitively, if the fates of paired items converge, then cueing should increase the proportion of items in the Both Better quadrant, but if the fates of paired items diverge, then cueing should increase the proportion of items in the One Better quadrants. To confirm this intuition, we simulated three different possible effects of cueing, whereby (a) paired cues benefit spatial memory for either picture independently (e.g. cue fates were unrelated), (b) improvement of spatial memory for one picture decreased the likelihood that the other improved (e.g. cue fates diverged), and c) improvement of spatial memory for one picture increased the likelihood the other improved (e.g. cue fates converged; Fig. 3B). The high- or low-reward picture was randomly chosen to be the first picture up as a candidate for improvement and its likelihood of improving was set to 1/9. For the three conditions we simulated, improvement for one picture (a) did not change the likelihood of spatial memory for the other picture improving (independence), (b) reduced the likelihood of it improving by a factor of 3 (likelihood = 1/27), or (c) increased the likelihood of it improving by a factor of 3 (likelihood = 1/3). The results of these simulations are shown in Fig. 3B.

2.8. Item versus competitor pre-nap accuracy bootstrapping procedure

TMR efficacy and competition could be affected by how well picture locations were learned before the nap. Specifically, competition, which we hypothesized would impair memory with TMR, should theoretically be strongest when the locations of both a picture and its competitor are both remembered well before the nap. Therefore, we assessed the influence of TMR on forgetting based on a picture's pre-nap spatial memory error and its competitor's pre-nap spatial memory error. First, for each paired picture, we took the picture's pre-nap spatial memory error and its competitor's pre-nap spatial memory error, and we plotted this as a point in 2-d space. We then slid a 150 × 150 pixel moving window around this space (Fig. 4B, left). For instance, the bin for 0–150 pixels for a picture and 0–150 pixels for its competitor would encompass the pair of Brad Pitt and Eiffel Tower if they had pre-nap errors of 70 pixels and 145 pixels, respectively. Note that, if a pair falls in the lower-left region of this 2-d space, this indicates that both the picture and its competitor were well-learned prior to the nap. Next, for each bin (i.e., each location of the moving window), we gathered up all of the pictures (both cued and uncued) that fell into this region of the 2-d space, and we used a *t*-test to compare the adjusted spatial forgetting scores for cued versus uncued pictures falling within this bin (Fig. 4B, right). We repeatedly moved this window until we had covered the

entire space. We then repeated these calculations 400 times after re-sampling participants with replacement (bootstrapping), producing 400 different *t* values for each bin. We calculated the mean and the 5th and 95th percentiles for the bootstrapped distribution of each bin (Fig. 4C); if the bootstrap distribution of *t* values reliably differs from zero, this indicates that the cued-uncued difference is reliable for that bin (shown in Fig. 4D). Next, we identified clusters of contiguous bins that reliably differed from zero (i.e., the middle 90% of the distribution from the 5th to 95th percentile is above or below zero). Finally, we repeated this entire procedure 400 times after randomly scrambling cued and uncued labels to find a null distribution of cluster sizes. This allowed us to determine whether the true cluster size exceeded the cluster size expected due to chance (using a $p < 0.05$ family-wise error threshold).

Cluster maps were calculated for all pictures together (i.e., lumping high-reward and low-reward pictures in the same analysis), as well as for high-reward and low-reward pictures separately. Note that, for analyses featuring all pictures, each pair is included twice: The high-reward picture stands as the picture of interest against the low-reward competitor and the low-reward picture stands as the picture of interest against the high-reward competitor. Also note that these analyses are not symmetric, because we are investigating spatial forgetting for particular pictures given that picture and its competitor's initial (pre-nap) accuracy. For instance, assume that Brad Pitt has an initial spatial error of 75 pixels and its competitor, the Eiffel Tower, has an initial spatial error of 45 pixels; assume also that Brad Pitt has an adjusted spatial forgetting value of 350 pixels, whereas Eiffel Tower has an adjusted spatial forgetting value of 15 pixels. When considering memory for Brad Pitt, the pair will be included in whichever bins include the point (75, 45), and we will use Brad Pitt's forgetting score (350); however, when considering memory for Eiffel Tower, the pair will be included in whichever bins include the point (45, 75), and we will use Eiffel Tower's forgetting score (15). We also included an analysis where we investigated a possible interaction between the cueing effect and reward. For this test, we contrasted the cued – uncued difference for high- versus low-reward pictures within the same regions of pixel space and proceeded with the same bootstrapping procedure as above.

2.9. EEG recording and pre-processing

Continuous EEG was recorded during the nap using Ag/AgCl active electrodes (Biosemi ActiveTwo, Amsterdam) in the same fashion at Northwestern and Princeton. Recordings were made at 512 Hz from 64 scalp EEG electrode locations. In addition, a vertical electrooculogram (EOG) electrode was placed next to the right eye, a horizontal EOG electrode was placed under the left eye, and an electromyogram (EMG) electrode was placed on the chin.

EEG data were processed using a combination of internal functions in EEGLAB (Delorme & Makeig, 2004) and custom-written scripts. Data were re-referenced offline to the average signal of the left and right mastoid channels and were down-sampled to 256 Hz. They were high-pass filtered at 0.1 Hz and low-pass filtered at 60 Hz in successive steps. Problematic channels were interpolated using the spherical method.

2.10. Electrophysiological analyses

Sleep stages were determined by an expert scorer according to standard criteria (Rechtschaffen & Kales, 1968). Table 1 shows the breakdown of stages for each condition as well as the number of cues occurring within each stage. Note that sleep-staging rules require assigning stages based on whichever stage is more prevalent within the 30-s epoch, which can result in sounds occurring in stages that were not the intended targets. Artifacts (large movements, blinks, arousals, and rare, large deflections in single channels) during sleep were marked separately in 5-s chunks following sleep staging.

To calculate oscillatory power, we first filtered separate signals into the theta (4–8 Hz), sigma (11–16 Hz) and beta (16–30 Hz) bands using a two-way, least-squares finite impulse response filter. Next, we calculated a root-mean-square (RMS) value for every time point using a moving window of 200 ms (using values 100 ms before and after each point) for each channel separately (Mölle, Bergmann, Marshall, & Born, 2011; Ngo, Martinetz, Born, & Mölle, 2013). We averaged RMS values within each condition for each participant, ignoring artefactual time segments, and calculated across-participant statistics for our planned contrasts of interest.

Table 1
Time in each sleep stage and number of sounds per stage for SPL and CPL conditions (min ± SEM). Differences between the conditions are shown below as *p* values.

Time in each stage (min)		Wake	S1	S2	S3	REM
SPL	Mean	26.48	9.22	26.77	28.30	4.12
	SEM	2.91	0.92	2.45	2.32	1.08
CPL	Mean	32.13	7.00	23.58	28.38	4.12
	SEM	3.09	0.83	2.02	1.64	1.00
p		0.19	0.08	0.32	0.98	1.00
Mean sounds per stage						
SPL	Mean	8.17	3.30	22.50	183.53	2.40
	SEM	3.37	1.29	5.08	22.15	1.68
CPL	Mean	3.27	1.97	12.10	199.40	3.97
	SEM	0.82	1.07	4.34	22.32	2.77
p		0.16	0.43	0.13	0.62	0.63

To test the reliability of differences in oscillatory power between conditions in situations where we did not have a strong *a priori* hypothesis about which time points were relevant (e.g., differences in beta power evoked by singular vs. paired TMR cues), we used a non-parametric permutation test procedure, first computing a bootstrap distribution of the difference in power between conditions at each time point. Next, we found clusters of consecutive time points whereby the central 90% of the bootstraps (5th or 95th percentile) differed from zero. Lastly, we computed a null distribution over cluster sizes by repeatedly permuting the conditions across pictures, re-running the bootstrap, and recording the maximum cluster size for each permutation. We considered a cluster to be significant if its size exceeded 95% of the null distribution (corresponding to a family-wise error rate of .05). After we identified relevant time windows, we used ANOVAs to explore how various factors (e.g., CPL/SPL, paired/singular, subsequent memory) modulated oscillatory power within those windows.

Analyses of electrophysiological predictors of subsequent memory relied on a pixel accuracy threshold to assess whether the locations of pictures were well-remembered or not. To avoid arbitrarily choosing this threshold pixel value, we based it on the results of the behavioral picture versus competitor analysis (see above section entitled, *Picture versus competitor pre-nap accuracy bootstrapping procedure*): In the CPL condition, we found a negative effect of cueing on spatial memory for paired pictures when both pictures in the pair had pre-nap spatial accuracy values ranging from 0 to 225 pixels (see Fig. 4; note that the bin labeled "150" encompassed accuracy values ranging from 75 to 225 pixels). Given the observed difference in behavioral cueing effects for pictures remembered (pre-nap) with accuracy above vs. below 225 pixels, we used 225 pixels in our electrophysiological analyses as the threshold for determining whether the locations of pictures were well-remembered or not.

3. Results

3.1. Competition during learning impaired pre-nap accuracy

We first assessed whether competition affected learning prior to sleep. Our design included a between-participants manipulation (CPL

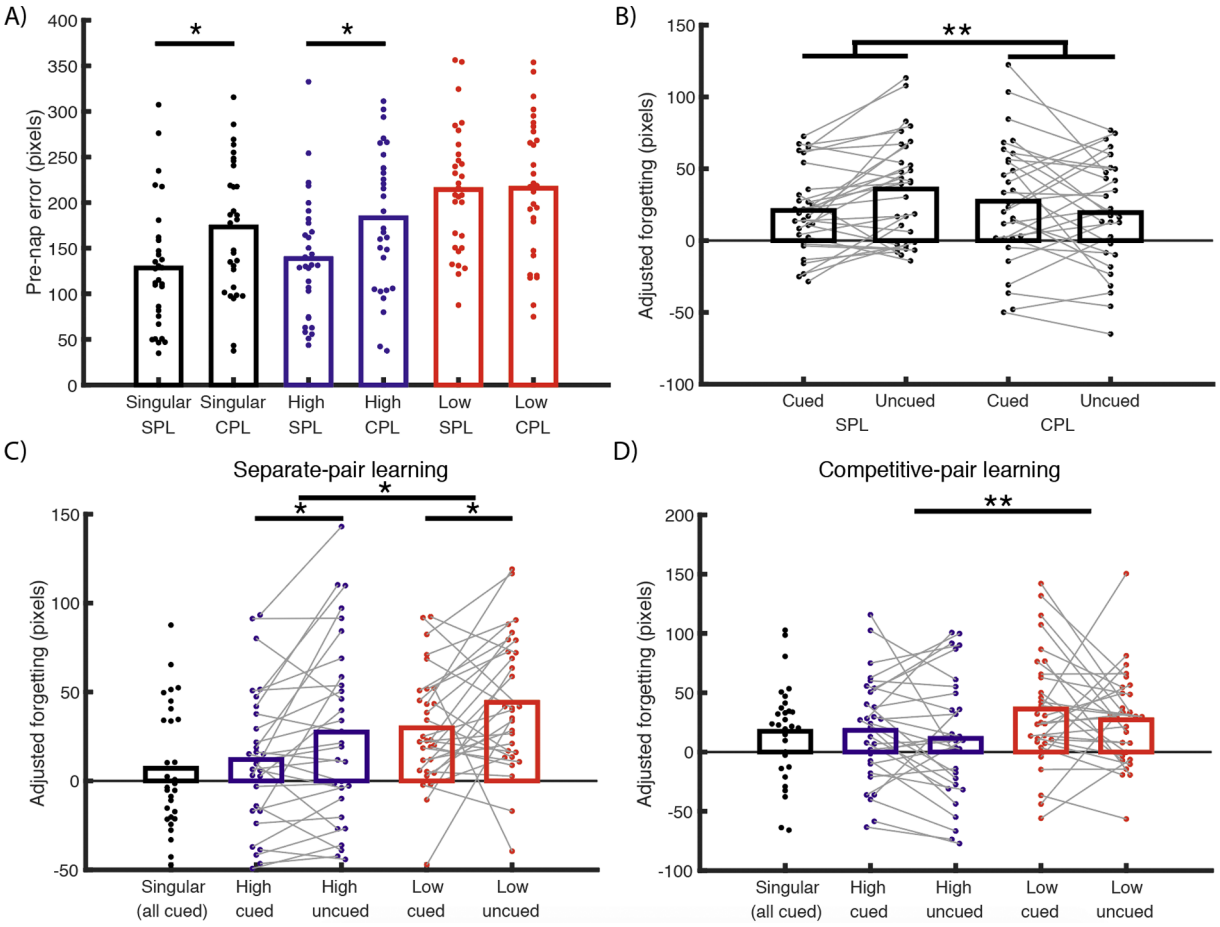

Fig. 2. Inter-item competition at encoding influences learning and targeted memory reactivation. Data are depicted using bee swarm plots, with rectangular box heights indicating means. (A) Competition negatively affected learning, as shown by differences in pre-nap error between the conditions. (B) Competition strongly altered the effectiveness of targeted memory cues, where lower forgetting indicates better memory retention. (C) Under SPL, reward reduced forgetting, and cueing reduced forgetting for both high and low rewards. (D) Under CPL, reward reduced forgetting, but cueing had no overall significant effect on memory. *: $p \leq 0.05$. **: $p < 0.01$.

vs. SPL) and three picture types: singular pictures (high-reward pictures associated with only a single sound), high-reward paired pictures, and low-reward paired pictures. We therefore submitted pre-nap spatial errors to a mixed, 2 (condition: CPL vs. SPL) × 3 (picture type: singular, high-reward paired, or low-reward paired) ANOVA. We found a significant main effect of picture type [$F(2,116) = 59.2$, $p < 0.001$], a marginal main effect of condition [$F(1,58) = 3.2$, $p = 0.08$], and a significant interaction [$F(2,116) = 7.8$, $p < 0.001$). As shown in Fig. 2A, follow-up t-tests revealed pre-nap spatial accuracy was better for the SPL than for the CPL condition for singular pictures [SPL: 128.4 ± 12.7 pixels, CPL: 173 ± 13.4, $t(58) = 2.4$, $d = 0.63$, $p = 0.02$] and for high-reward paired pictures [SPL: 138.7 ± 12.2, CPL: 183.4 ± 14.0, $t(58) = 2.4$, $d = 0.62$, $p = 0.02$] but not for low-reward paired pictures [SPL: 214.4 ± 12.6, CPL: 215.9 ± 13.9, $t(58) = 0.08$, $d = 0.01$, $p = 0.94$]. This effect of CPL vs. SPL on pre-nap spatial accuracy for singular picture-location associations was unexpected. We speculate that pair encoding might have been more difficult in the CPL condition due to increased competition, thereby explaining why pre-nap memory was lower for high-reward pair items in CPL compared to SPL. Additionally, if participants realized they were not encoding CPL pairs quite as well on average, they may have taken more time away from singular item rehearsal to rehearse the pairs in the CPL condition, thereby explaining why pre-nap singular item memory was worse in CPL compared to SPL.

3.2. Competition during learning influenced the effects of targeted memory reactivation

Our primary procedural manipulations were (1) altering the amount of competition between paired pictures during learning by either presenting them competitively (CPL condition) or separately (SPL condition), (2) administering TMR cues for only half of the pairs, thus creating cued and uncued conditions, and (3) manipulating reward for each paired picture to be either high or low. Our primary dependent measure of adjusted spatial forgetting across the nap was computed as post-nap error minus pre-nap error, after regressing out the effects of pre-nap error (see Methods; Fig. 1B). Greater positive values of this adjusted measure indicate more forgetting and therefore worse memory retention.

We first asked how these three main factors interacted by running a condition (SPL vs. CPL) × cue status (cued vs uncued) × paired picture reward status (high vs. low) ANOVA on adjusted spatial forgetting values for paired pictures. As expected, there was a significant main effect of reward [$F(1,58) = 14.24$, $p < 0.001$], indicating better retention for high- than low-reward picture-locations. There were no significant main effects of condition [$F(1,58) = 0.37$, $p < 0.56$] or cueing [$F(1,58) = 0.84$, $p < 0.36$]. Additionally, as predicted, we found a significant interaction between condition and cueing [$F(1,58) = 9.13$, $p = 0.004$], indicating that competition affected TMR efficacy. There

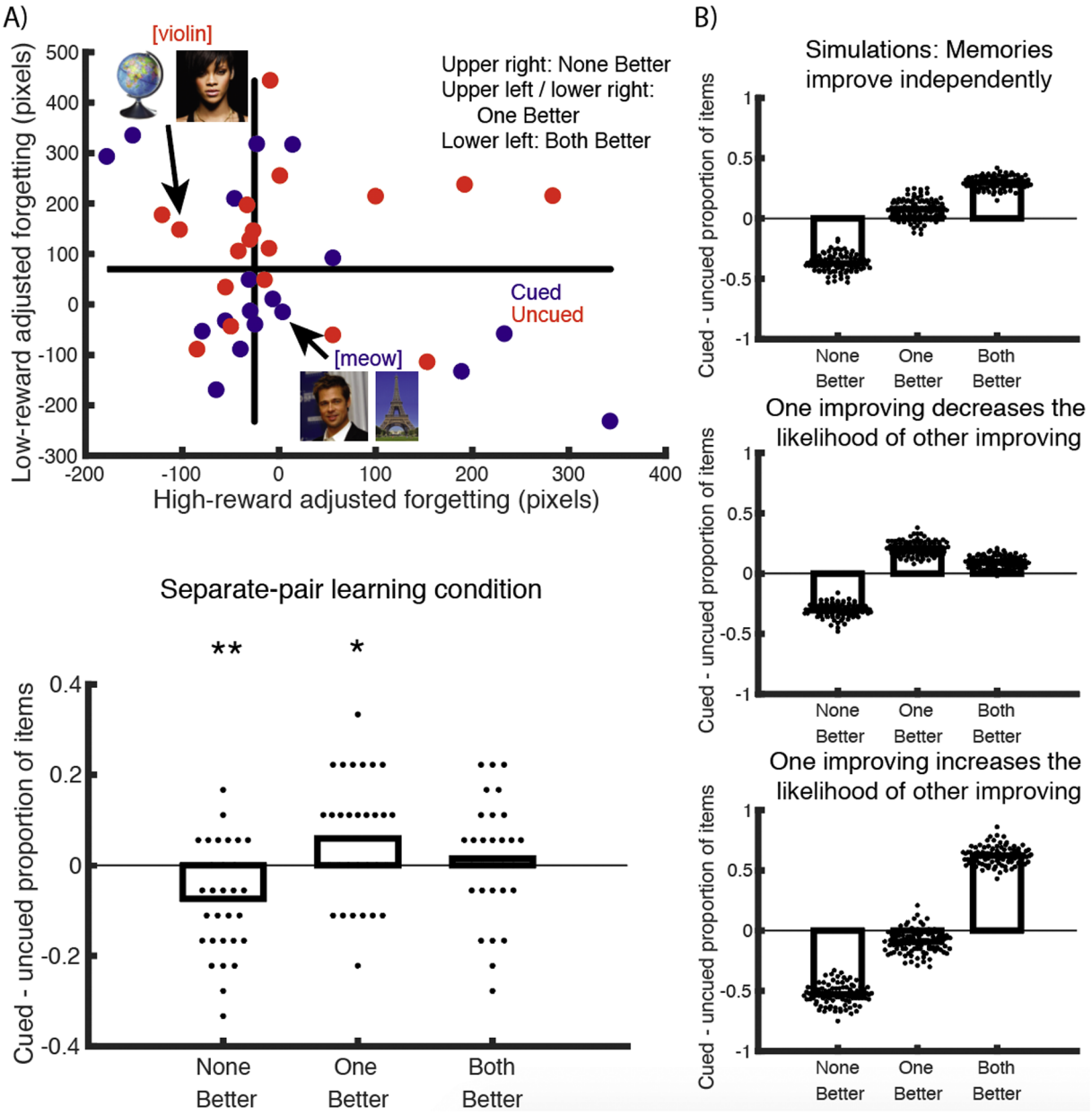

Fig. 3. Under separate pair learning, cueing helps spatial memory for one picture, but not both. (A) The upper panel shows median adjusted spatial forgetting values for high- and low-reward pictures (horizontal and vertical lines) for a single example participant, as well as the adjusted spatial forgetting scores for particular cued and uncued pairs (quadrants were defined by the adjusted spatial forgetting values for each of the paired pictures being better or worse than their median). If a pair fell in the upper-right quadrant, that indicated that neither of the adjusted spatial forgetting values for the pair were better than the median *(None Better)*, pairs in the upper left and lower right indicated one of the adjusted spatial forgetting values was better than the median *(One Better)*, and pairs in the lower left indicated both of the adjusted spatial forgetting values were better (*Both Better*). The lower panel shows the proportion of cued pairs minus uncued pairs falling within each group defined above. Across participants, there were significantly fewer cued than uncued pairs in the None Better group and significantly more cued than uncued pairs in the One Better group. *: $p \leq 0.05$. **: $p < 0.01$. (B) We ran simulations between adjusted spatial forgetting for paired pictures under different assumptions of how cues affect spatial memory for pictures within pairs. These simulations show that the actual results fit best with the assumption that when spatial memory for one picture improves, the other is less likely to improve.

were no other significant interactions [reward × cueing: $F(1,58) = 0.045$, $p = 0.83$; reward × condition: $F(1,58) = 0.002$, $p = 0.96$; reward × cueing × condition: $F(1,58) = 0.006$, $p = 0.94$]. Therefore, there was no support for our predicted three-way interaction between these factors.

Follow-up analyses on the condition and cueing interaction (collapsing across reward) showed the cueing effect was larger in the SPL condition than the CPL condition [in pixel mean ± SEM, SPL cued – uncued error: −14.9 ± 6.0, CPL cued – uncued error: 7.9 ± 7.3, $t(59) = 3.0$, $d = 0.78$, $p = 0.004$], demonstrating that competition decreases the efficacy of TMR (Fig. 2B). These differences do not depend on our approach of regressing out pre-nap error scores – they are still significant when using raw, rather than adjusted, forgetting measures [in pixel mean ± SEM, SPL cued – uncued error: −15.2 ± 5.2, CPL cued – uncued error: 7.8 ± 6.0, $t(59) = 2.9$, $d = 0.75$, $p = 0.005$]. To ensure differences in TMR efficacy were not merely driven by pre-nap spatial memory differences between the conditions, we randomly resampled participants without replacement ($N = 18$–28) from both the CPL and SPL groups to find instances in which there was no pre-nap difference in high reward spatial error between CPL and SPL ($t < 0.05$

for that instance). We found the interaction (greater cueing effect in SPL than CPL) still held in each of 100 instances meeting this condition as determined by a significant t value in each (t mean = 2.5, standard error = 0.05, range = 1.4 to 3.7). There was no overall bias in pre-nap memory across the 100 instances, as measured by a null effect in a t-test (across the 100 instances) of the pre-nap score differences between the conditions [$t(99) = 0.07$, $p = 0.95$]. Therefore, pre-nap memory differences between the conditions cannot explain the differences in TMR efficacy between CPL and SPL.

Given that we had specific predictions about how reward would interact with cueing within each competition condition, we next assessed the effects of reward priorities and TMR on memory retention using a two-way, repeated-measures ANOVA for each competition condition separately. For SPL, we did not expect an interaction between reward and cueing, and the data fit with this prediction: Spatial memory was better for high-reward pictures than low-reward pictures [$F(1,29) = 6.0$, $d_z = 0.45$, $p = 0.02$] and spatial memory was better for cued pictures than uncued pictures [$F(1,29) = 11.0$, $d_z = 0.61$, $p = 0.002$], but there was no interaction between the conditions [$F(1,29) = 0.01$, $d_z = 0.02$, $p = 0.91$; Fig. 2C]. Follow-up t-tests indicated TMR benefited memory in the high-reward condition [cued: 12 ± 7.0 pixels, uncued: 27.4 ± 9.3, $t(29) = 2.6$, $d_z = 0.48$, $p = 0.01$] and marginally in the low-reward condition [cued: 29.8 ± 5.8, uncued: 44.2 ± 6.9, $t(29) = 2.0$, $d_z = 0.37$, $p = 0.052$]. For CPL, we predicted an interaction whereby cueing would have opposite effects on spatial memory for high-reward and low-reward pictures; this prediction was not confirmed: Spatial memory was better for high-reward pictures than low-reward pictures [$F(1,29) = 8.9$, $d_z = 0.55$, $p = 0.006$], but there was no effect of TMR [$F(1,29) = 1.7$, $d_z = 0.24$, $p = 0.20$] or interaction [$F(1,29) = 0.03$, $d_z = 0.03$, $p = 0.86$; in pixels, high cued: 18.4 ± 8.0, high uncued: 11.6 ± 9.4, low cued: 36.4 ± 8.9, low uncued: 27.3 ± 7.2; Fig. 2D].

3.3. Under separate pair learning, cueing tended to help one picture-location, but not both

Under SPL, TMR benefited both spatial memory for both high- and low-reward pictures. However, the above analyses did not examine whether spatial memory improvements for one picture occurred independently of effects on its paired picture. For instance, a TMR benefit for Brad Pitt's location could tend to occur along with a TMR benefit for the Eiffel Tower. If spatial memory improvement for one picture increases the likelihood of spatial memory improvement for another picture, their fates converge; conversely, if it decreases that likelihood, their fates diverge. To assess whether fates converged or diverged, we calculated the median adjusted spatial forgetting value for high- and low-reward pictures separately. Each pair fell into one of four quadrants depending on whether the adjusted spatial forgetting values for the high-reward and low-reward pictures in the pair were better or worse than their respective median values (Fig. 3A). Based on this rough categorization, each pair can be labeled according to whether adjusted spatial forgetting was better than the median for neither, one, or both pictures in the pair. If cueing improved spatial memory for one picture and not the other, we would expect fewer cued pairs in the upper right (*None Better*) and more cued pairs in the upper left and lower right quadrants (*One Better*), whereas if it improved spatial memory for both pictures of a pair, there should be fewer cued pairs in the upper right and more cued pairs in the lower left *(Both Better)*. We then measured the number of cued versus uncued pairs in each bin using within-participant t-tests. We found significantly fewer cued than uncued pairs in the None Better group [$t(29) = 3.3$, $d_z = 0.61$, $p = 0.002$], significantly more cued than uncued pairs in the One Better group [$t(29) = 2.39$, $d_z = 0.44$, $p = 0.02$], and no difference than in the Both Better group [$t(29) = 0.63$, $d_z = 0.11$, $p = 0.53$].

We next ran simulations (see Methods; Fig. 3B) on the data under three assumptions: spatial memory improvements for one picture (1) do not affect the likelihood that spatial memory improves for the other picture, (2) decrease the likelihood the other improves, or (3) increase the likelihood the other improves. The simulations involved treating the uncued data from the SPL condition as a "baseline" against which cueing could impact results under the various assumptions. Our actual data were most consistent with the simulation where we assumed that cueing improvements are negatively correlated within a pair: in this simulation, we found far fewer cued than uncued pairs in the None Better group (mean difference in proportion: −0.30 ± 0.006, $p < 0.001$), far more cued than uncued pairs in the One Better group (0.22 ± 0.007, $p < 0.001$), and only slightly more cued than uncued pairs in the Both Better group (0.083 ± 0.004, $p < 0.001$). Note that the goal of the simulations was to capture the qualitative nature of the data under various assumptions, so statistical significance, though shown, was not critical.

Lastly, we also ran the quadrant analyses for the CPL condition. It did not produce significant results [None Better: cued 0.27 ± 0.02, uncued: 0.24 ± 0.02, $t(29) = 1.08$, $d_z = 0.20$, $p = 0.29$; One Better: cued 0.48 ± 0.03, uncued: 0.50 ± 0.02, $t(29) = 0.71$, $d_z = 0.13$, $p = 0.49$; Both Better: cued, 0.25 ± 0.02, uncued: 0.26 ± 0.01, $t(29) = 0.51$, $d_z = 0.09$, $p = 0.62$].

3.4. Under competitive pair learning, cueing impaired spatial memory when both of the picture-location associations were well-learned prior to the nap

Contrary to what was observed under SPL, we found no cueing benefit under CPL, suggesting competition negatively affects TMR efficacy. To follow up on this point, we measured how these effects were modulated by pre-nap accuracy. We hypothesized that competition would be strongest when the locations of both pictures in the pair were well-learned pre-nap; in this case, we might see weakening of competing memories in response to cues (i.e., a negative TMR effect).

To test this hypothesis, we investigated whether spatial memory retention differed for cued and uncued pictures as a function of both the pre-nap spatial accuracy of a picture and its competitor (Fig. 4; see Methods). For each paired picture, we plotted the pre-nap spatial error values of the picture and its competitor as a point in 2D space (x value = pre-nap spatial error for the picture; y value = pre-nap spatial error for the competitor), and then grouped these points into bins defined by a moving window of 150 × 150 pixels (bin ± 75 pixels, step = 4 pixels; Fig. 4B). For each bin, we then calculated the t-statistic between the amount of adjusted spatial forgetting for cued and uncued pictures within that bin. We repeated this procedure by randomly resampling participants with replacement (bootstrapping) 400 times. We determined significance in two steps. First, we sorted all 400 bootstraps and identified clusters of contiguous bins that all differed from zero at the 90% confidence level (between the 5th and 95th percentile). Second, we scrambled the cued and uncued labels 400 times and repeated the bootstrapping procedure, finding the largest cluster size in each scrambled permutation to determine a $p < 0.05$ threshold for significant cluster size. Any true cluster size exceeding this threshold was deemed significant.

Our first analysis combined spatial memory for both high- and low-reward pictures. Each pair contributed twice to this analysis: once with the high-reward picture as the picture of interest (i.e., the picture whose adjusted spatial forgetting was measured) and once with the low-reward picture as the picture of interest. In other words, both pictures acted in turn as the picture of interest and the competitor. The mean of these bootstraps is shown in Fig. 4C and the cluster of contiguous bins with their middle 90% interval differing from zero is shown in Fig. 4D. This analysis produced a significant cluster indicating a TMR impairment in the range in which the locations of the picture and its competitor were well-remembered pre-nap (cluster size: 3693 bins; $p = 0.005$; Fig. 4E); the mean difference in adjusted spatial forgetting for cued vs. uncued pictures was 29 pixels, averaging across bins in the significant cluster. We next looked at spatial memory for high-reward

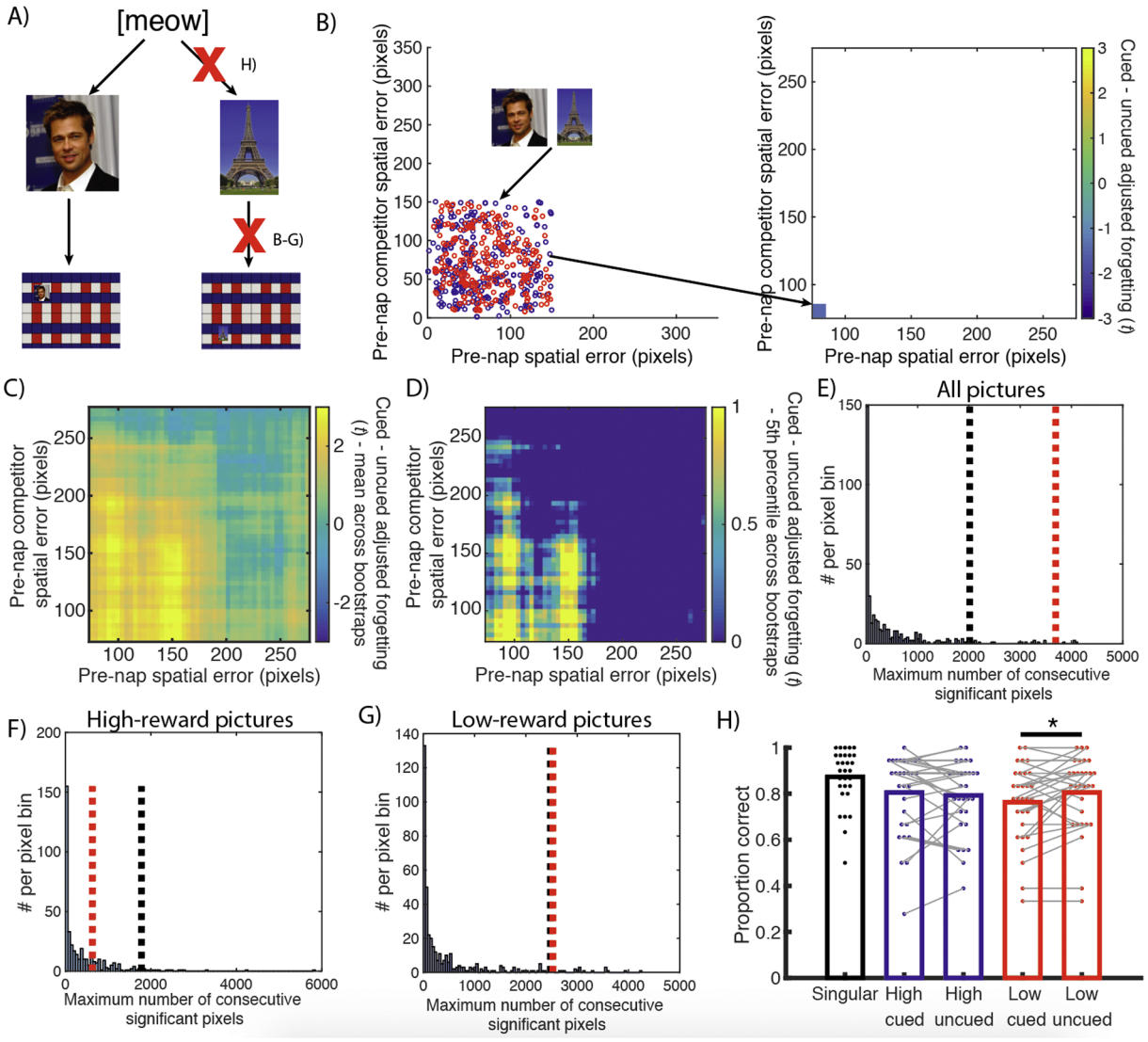

Fig. 4. Under competitive pair learning, cueing impairs spatial memory when the locations of both pictures are well-learned pre-nap, and also impairs sound-picture memory. (A) Schematic showing two ways cueing could impair memories: by weakening associations between the sound and picture or by weakening associations between the picture and its location. (B) Schematic of analysis relating pre-nap accuracy to cueing effects. We binned pictures according to their pre-nap spatial accuracy and the pre-nap spatial accuracy of their competitor. Each bin contained adjusted spatial forgetting values for all cued and uncued pictures within a moving window (left); within each bin, we calculated a *t*-statistic contrasting forgetting for cued and uncued pictures (right). (C–D) Using a bootstrap analysis, we found a large cluster of bins that showed a negative TMR effect (more forgetting for cued than uncued picture locations) in the CPL condition; this negative TMR effect is evident for pictures where the locations of both the picture itself and its paired picture (competitor) were well-learned prior to the nap. The mean cued-uncued differences in adjusted spatial forgetting across bootstraps are shown in (C). Bins where the lower 5th percentile of bootstraps fall above zero are shown in (D). (E–G) Cluster size (red line) exceeds the size expected due to randomly shuffling the labels (black line) when (E) combining spatial memory for high reward pictures against their low reward competitors and low reward pictures against their high reward competitors, as well as (G) low reward pictures considered against their high reward competitors alone, but not when high-reward pictures were considered alone (F). (H) Cueing during CPL impaired recall of previously overlearned sound-picture associations for pictures that were assigned to the low-reward condition. * indicates $p < 0.05$.

pictures and low-reward pictures separately. When high-reward pictures were considered against their low-reward competitor, we found no significant effect (cluster size: 669 bins; p = 0.24; Fig. 4F), but when low-reward pictures were considered against their high-reward competitor, we found a significant cluster indicating cueing impairments (cluster size: 2484 bins; $p = 0.045$; Fig. 4G); the mean difference in adjusted spatial forgetting for cued vs. uncued pictures was 40 pixels, averaging across bins in the significant cluster. There was no interaction between the conditions, as assessed by a high-reward – low-reward spatial forgetting contrast using the same analysis (cluster size: 10 bins; < 10th percentile relative to the null cluster size distribution). Given the somewhat arbitrary choice of using a 150-pixel moving window, we also ran the same analyses using a 100-pixel window. We again found strong significance when considering both pictures together (cluster size: 2552 bins; $p = 0.01$), not when considering high-reward pictures alone (cluster size: 504 bins; $p = 0.38$), and again when considering low-reward pictures alone (cluster size: 2212 bins; $p = 0.015$). The same analyses applied to the SPL condition showed a broad range of bins for which cueing was beneficial for memory, meaning it was broadly in the opposite direction of the CPL effect above, but there was no significant cluster. Together, these results demonstrate that under conditions of competitive learning and strong initial spatial memory for more than one picture, TMR can cause forgetting.

3.5. Under competitive pair learning, cueing impaired overlearned sound-picture memories

After the final post-nap spatial test, participants took another test to verify that they still retained the sound-picture associations learned in Phase 1. We expected recall to be at or near ceiling, but also included a *post-hoc* analysis of post-nap memory (not of pre-post differences, because no sound-picture test was given prior to the nap). Consistent with the idea that cues linked with more pictures endure more interference, singular associations were better remembered than all other categories under CPL (proportion correct for singular pictures: 0.87 ± 0.02, all $p < 0.005$; Fig. 4H). To test whether cueing impaired paired sound-picture memories under CPL, we ran a repeated-measures, cueing status (cued vs. uncued) × reward status (high vs. low) ANOVA. We found no main effect of cueing [$F(1,29) = 1.15$, $p = 0.29$] or reward [$F(1,29) = 0.87$, $p = 0.36$], but there was a marginal interaction [$F(1,29) = 4.0$, $p = 0.055$]. Follow up *t*-tests indicated that cues impaired sound-picture memory for low-reward pictures [cued: 0.76 ± 0.03, uncued: 0.81 ± 0.03, $t(29) = 2.22$, $d_z = 0.41$, $p = 0.03$] but not high-reward pictures [cued: 0.81 ± 0.03, uncued: 0.79 ± 0.03, $d_z = 0.12$, $p = 0.52$]. These findings are consistent with the previous results that cueing impaired memory, especially for low-reward pictures. In the SPL condition, we also found better memory for the singular category (proportion correct for singular pictures: 0.88 ± 0.02, all $p < 0.005$), but found no other effects [main effect of cueing: $F(1,29) = 0.18$, $p = 0.68$; main effect of reward: $F(1,29) = 2.2$, $p = 0.15$; interaction: $F(1,29) = 0.05$, $p = 0.83$; high cued: 0.79 ± 0.03, high uncued: 0.79 ± 0.03, $t(29) = 0.14$, $d_z = 0.02$, $p = 0.88$; low cued: 0.80 ± 0.02, low uncued: 0.81 ± 0.03, $t(29) = 0.48$, $d_z = 0.08$, $p = 0.63$]. Thus, these tests provided converging evidence that low-reward information was weakened under CPL.

3.6. Post-cue beta power differentiated between paired and singular pictures, but not between CPL and SPL

Based on previous studies showing greater levels of beta power in situations with greater competition (Oyarzún et al., 2017; Waldhauser, Johansson, & Hanslmayr, 2012), we investigated whether post-cue beta power was modulated by competition in our study. Specifically, we predicted that post-cue beta would be higher in the paired condition (due to competition between pictures within a pair) than in the singular condition. Also, within the paired condition, we expected greater competition (and thus greater post-cue beta) in the CPL condition than the SPL condition.

First, we addressed the paired vs. singular prediction. In keeping with this prediction, we found that, in both the CPL and SPL conditions, post-cue beta power was higher for paired than singular sounds 250–750 ms across multiple electrodes, maximal over electrode FCz in each condition (Fig. 5A). To verify that this FCz difference was reliable (correcting for the fact that we were looking at multiple time points), we used a bootstrapping procedure to determine contiguous segments of time in which the central 90% of the beta power differences between singular and paired pictures differed from zero; this bootstrapping analysis collapsed across CPL and SPL. We calculated the likelihood that a time segment that large could occur by chance using a $p < .05$ threshold across the whole interval by scrambling the conditions within each participant. This analysis confirmed that paired cues had reliably higher post-cue beta power than singular cues at FCz around the same early time interval (in relation to the size of clusters from the null distribution: $p = 0.01$; Fig. 5A).

Having identified the relevant time window, we explored whether post-cue beta was modulated by CPL vs. SPL; to allow for the possibility of interactions between paired vs. singular and CPL vs. SPL, we ran a mixed ANOVA on mean beta power over FCz from 250 to 750 between cue type (singular vs. paired) and competition condition (CPL vs. SPL). We found a main effect of cue type [$F(1,57) = 63.6$, $p < 0.001$] and no main effect of competition condition [$F(1,57) = 0.73$, $p = 0.40$] or interaction [$F(1,57) = 0.53$, $p = 0.47$; Fig. 5A]. These results do not provide support for our prediction that CPL vs. SPL should modulate post-cue beta.

We also ran an analysis to assess the possibility that pre-nap differences in memory between singular and paired sounds might account for these early beta power differences. In this analysis, we tried to match the average pre-nap error on singular items against the average error of the two paired items. Without matching, singular items had significantly lower error than the average of paired items (in pixels, singular: 150.9 ± 9.6; average paired: 188.1 ± 8.7; $t(59) = 7.9$, $dz = 1.0$, $p < 0.001$). After resampling subjects to minimize differences in pre-nap error (see *Methods*), we were able to equate singular and paired items in pre-nap error ($p = 0.44$), but there was still a significant difference in beta power between 250 and 750 ms in every one of the resampled instances ($p < 0.01$).

3.7. Post-cue beta power negatively predicted subsequent memory

Beta power has also been found to negatively predict subsequent memory (Hanslmayr, Spitzer, & Bäuml, 2009; Waldhauser et al., 2012). To test this relationship in our data, we began by investigating the picture-location associations most likely to be reactivated: those corresponding to singular pictures whose locations were well-remembered before the nap (≤225 pixel error, see Methods), a condition we refer to as singular-R. We expected competition for these picture-location associations to be low on average, but we also expected there to be variance across them in the level of competition – singular picture locations can compete to different degrees with other studied associations, even if those associations were linked to other sounds; we hypothesized that this picture-by-picture variance would be registered in beta power and would predict memory. Specifically, we asked whether beta power negatively predicted whether picture-location associations remained well-remembered after the nap when combining both CPL and SPL conditions (we used "singular-R-R" to indicate pictures whose locations were well-remembered after the nap and "singular-R-NR" to indicate pictures whose locations were not well-remembered after the nap, respectively; to split pictures into these groups, we used the same 225-pixel-error criterion that we applied to pre-nap error). Individuals without any trials in the singular-R-NR condition were dropped from the analysis ($N = 4$ for SPL, $N = 4$ for CPL). Indeed, early beta power was significantly higher for not-remembered than remembered picture locations (in relation to the size of clusters from the random (null) distribution: $p = 0.03$; Fig. 5B). A mixed ANOVA performed on mean beta power over FCz from 250 to 750 between subsequent memory (singular-R-R vs. singular-R-NR) and competition condition (CPL vs. SPL) revealed a significant main effect of subsequent memory [$F(1,50) = 55.7$, $p < 0.001$], no main effect of competition condition [$F(1,50) = 0.6$, $p = 0.44$], and no interaction [$F(1,50) = 0.48$, $p = 0.49$; Fig. 5B].

Finally, we asked whether beta power also predicted forgetting in the paired condition. Specifically, we asked whether post-cue beta power differed for subsequently remembered versus subsequently forgotten paired picture locations that were initially well-remembered prior to the nap [paired-R-R vs. paired-R-NR]. Note that this analysis combined high- and low-reward picture locations. Individuals without trials in both paired-R-R and paired-R-NR conditions were dropped from the analysis ($N = 7$ for SPL, $N = 3$ for CPL). Indeed, early beta power was significantly higher for paired-R-NR than paired-R-R picture locations ($p = 0.02$; Fig. 5C). A mixed ANOVA performed on mean beta power over FCz from 250 to 750 between subsequent memory (paired-R-R vs. paired-R-NR) and competition condition (CPL vs. SPL) revealed a significant main effect of subsequent memory [$F(1,48) = 51.6$, $p < 0.001$], no main effect of competition condition [$F(1,48) = 1.87$, $p = 0.18$], and no interaction [$F(1,48) = 1.31$, $p = 0.26$; Fig. 5C]. Based on our behavioral results, we did not expect any interactions between reward and cueing, so we did not include reward in our main

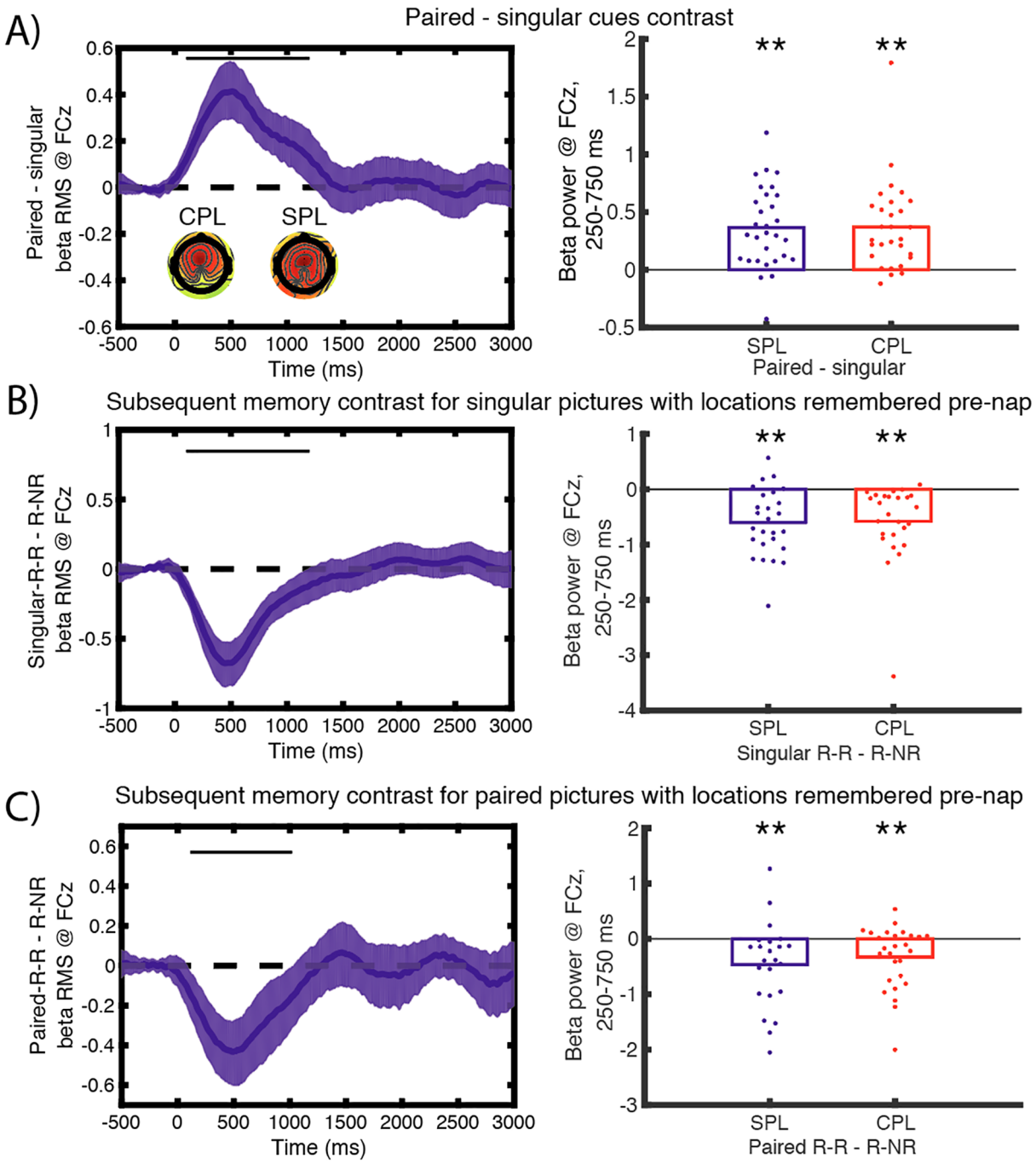

Fig. 5. Post-cue beta oscillations increase with competition and negatively predict subsequent memory. Left plots show the mean surrounded by the central 90% of bootstraps for contrasts combining data from the SPL and CPL conditions. Right plots show mean beta power contrasts from 250 to 750 ms over FCz for SPL and CPL separately. (A) Contrast of beta power for paired versus singular sounds. Left inset: topographical maps of each condition. (B) Contrast of beta power for subsequently remembered versus forgotten picture locations, focusing on singular pictures whose locations were well-remembered pre-nap. (C) Contrast of beta power for subsequently remembered versus forgotten picture locations, focusing on paired pictures whose locations were well-remembered pre-nap. ** indicates $p < 0.01$.

ANOVA. Also, including reward necessitates dropping a large number of participants (14 each from CPL and SPL) because of missing cells. Nonetheless, for completeness, we also re-ran the ANOVA also including reward (high, low) as a factor along with subsequent memory and competition condition. The main effect of subsequent memory remained significant [$F(1,30) = 8.59, p = 0.006$] but none of the two-way or three-way interactions were significant [competition condition: $F(1,30) = 0.05, p = 0.82$; reward: $F(1,30) = 0.10, p = 0.76$; competition condition × reward: $F(1,30) = 0.67, p = 0.42$; competition condition x memory: $F(1,30) = 0.026, p = 0.87$; reward × memory: $F(1,30) = 0.40, p = 0.53$; 3-way interaction: $F(1,30) = 2.25, p = 0.14$].

We also conducted separate analyses to assess the possibility that pre-nap differences between singular-R-R and singular-R-NR items accounted for these differences in beta power. First, there do appear to be differences in initial memory for items falling within these bins. After dropping subjects without any trials in both conditions, singular items in the R-R and R-NR groups differed (in pixels, singular-R-R: 82.5 ± 3.8; singular-R-NR: 111.7 ± 4.9; $t(53) = 5.1$, $d_z = 0.69$, $p < 0.001$), such that singular-R-R items were initially better-remembered. We therefore resampled subjects so as to equate the pre-nap

differences for singular item memory in the R-R and R-NR groups. After this resampling method, there were no longer significant differences in pre-nap memory between singular-R-R and singular-R-NR items ($p = 0.49$). However, there were still differences in the beta range between 250 and 750 ms in every instance ($p < 0.01$). Paired items in the R-R and R-NR groups also differed significantly (in pixels, paired-R-R: 90.3 ± 3.0; paired-R-NR: 122.7 ± 2.6; t(59) = 9.6, dz = 1.25, p < 0.001). However, we were unable to match the conditions for pre-nap accuracy to run these analyses, as these differences persisted in all except four subjects.

3.8. Post-cue sigma power predicted subsequent memory

Based on previous studies, we hypothesized that sigma power approximately 1000–1500 ms post-cue would positively predict retention (Antony et al., 2018; Farthouat, Gilson, & Peigneux, 2017; Groch, Schreiner, Rasch, Huber, & Wilhelm, 2017; Lehmann et al., 2016; Schreiner, Lehmann et al., 2015). As fast spindles tend to correlate with subsequent memory (Antony and Paller, 2017), we chose the midline centroparietal location (CPz) for spindle power *a priori* as it is the scalp location where fast spindle power is maximum (Andrillon et al., 2011; Mölle et al., 2011; Peter-Derex, Comte, Mauguière, & Salin, 2012). For this analysis, we focused on the same behavioral contrasts as above: First, we looked at singular pictures whose locations were well-remembered pre-nap and then remembered or forgotten post-nap (singular-R-R vs singular-R-NR); next, we looked at paired pictures whose locations were well-remembered pre-nap and then remembered or forgotten post-nap (paired-R-R vs. paired-R-NR).

First, we submitted sigma power to a mixed, condition (SPL vs. CPL) × memory (singular-R-R vs singular-R-NR) ANOVA (Fig. 6A). Individuals without any trials in the singular-R-NR condition were dropped from the analysis ($N = 4$ for SPL, $N = 4$ for CPL). We found a significant effect of memory [$F(1,50) = 15.1$, $p < 0.001$], no main effect of condition [$F(1,50) = 0.33$, $p = 0.57$], and no interaction [$F(1,50) = 0.03$, $p = 0.86$]. To look for other time windows that might show an effect, we submitted these analyses to the same bootstrapping procedure that was described above. We found the significant interval extended beyond 1000–1500 ms, ranging from 772 to 2580 ms ($p = 0.005$). The brief negative time segment was not significant ($p = 0.17$).

We next asked whether this signal predicted subsequent memory for paired pictures whose locations were well-remembered pre-nap (Fig. 6B). We submitted sigma power to a mixed, condition (SPL vs. CPL) x memory (paired-R-R vs. paired-R-NR) ANOVA. Individuals without trials in both conditions were dropped from the analysis ($N = 7$ for SPL, $N = 3$ for CPL). We found a marginal main effect of memory [$F(1,29) = 2.9$, $p = 0.09$], no main effect of condition [$F(1,29) = 1.6$, $p = 0.21$], and no interaction [$F(1,29) = 0.82$, $p = 0.37$]. For completeness, we also re-ran the ANOVA including reward (high, low) as a factor along with subsequent memory and competition condition; this necessitated dropping 14 participants each from CPL and SPL because of missing cells. The main effect of subsequent memory remained marginal [$F(1,30) = 3.43$, $p = 0.074$] and none of the two-way or three-way interactions were significant [competition condition: $F(1,30) = 1.72$, $p = 0.2$; reward: $F(1,30) = 0.64$, $p = 0.43$; competition condition × reward: $F(1,30) = 0.48$, $p = 0.50$; competition condition × memory: $F(1,30) = 1.58$, $p = 0.22$; reward × memory: $F(1,30) = 0.40$, $p = 0.53$; 3-way interaction: $F(1,30) = 0.49$, $p = 0.49$]. To look for other time windows that might show an effect, we submitted these analyses to the same bootstrapping procedure that was described above. We found no other time segments showing significance at the $p < 0.05$ level.

We again conducted separate analyses to assess the possibility that pre-nap differences between singular-R-R and singular-R-NR items accounted for these differences in sigma power. After conducting a similar resampling method as above, there were no longer significant differences in pre-nap memory between singular-R-R and singular-R-NR items ($p = 0.49$). However, there were still differences in the sigma range between 1000 and 1500 ms in every instance ($p < 0.01$). We were again unable to match the conditions for pre-nap accuracy between paired-R-R and paired-R-NR items, as these differences persisted in all except four subjects.

In sum, post-cue sigma power positively predicted subsequent spatial memory for singular pictures; this signal trended in the same direction but was not significantly predictive of subsequent spatial memory for paired pictures. We also ran a post-hoc bootstrap test to directly compare the sigma-power subsequent spatial memory effects for singular and paired pictures; we found that the subsequent memory effect was significantly larger for singular than paired pictures from 1100 ms to 2004 ms ($p = 0.0475$).

3.9. Post-cue theta power did not predict competition or subsequent memory

Previous studies have linked competition with theta power during wake over left parietal electrodes (Hanslmayr, Staudigl, Aslan, & Bäuml, 2010) and subsequent memory effects after sleep with post-cue (~500–1000 ms) theta power over right central (Schreiner and Rasch, 2014; Schreiner, Lehmann et al., 2015), left frontal (Schreiner, Lehmann et al., 2015), and centroparietal locations (Schreiner, Göldi, & Rasch, 2015). Therefore, we submitted theta power from 500 to 1000 ms over P5 (left parietal), C4 (right central), CPz (centroparietal), and F1 (left frontal) electrodes to mixed, condition (CPL vs. SPL) by cue type (singular vs. paired) by ANOVAs. We also submitted theta power in the above channels to mixed, condition (CPL vs. SPL) by singular subsequent memory (singular-R-R vs. singular-R-NR) and paired subsequent memory (paired-R-R vs. paired-R-NR) ANOVAs. We found no significant main effects for any ANOVA at the uncorrected $p < 0.05$ level.

4. Discussion

Retrieval cues can cause multiple memories to be activated simultaneously, leading to competition and memory weakening (Lewis-Peacock and Norman, 2014; Norman et al., 2007). Here, our manipulation of competition between paired pictures during learning strongly modulated the effects of TMR during sleep. Under the separate-pair learning (SPL) condition, when the locations of pictures sharing a common sound were learned separately, TMR improved spatial memory. However, under the competitive-pair learning (CPL) condition, when the locations of pictures sharing a common sound were learned in succession and rehearsed competitively, TMR produced no overall benefit for spatial memory and even impaired spatial memory when both members of a pair had high pre-nap accuracy (i.e., when competition between the memories was presumably strongest).

Reactivation is generally regarded to benefit memory, even in some cases when it is task-irrelevant (Kuhl, Johnson, & Chun, 2013); however, other prior work has shown that moderate reactivation weakens memory relative to no reactivation at all, whereas only strong reactivation results in strengthening (Lewis-Peacock and Norman, 2014; Newman and Norman, 2010; Norman et al., 2007; Poppenk and Norman, 2014). We speculate that weakening occurred because two picture-location memories simultaneously came to mind, but neither could become fully activated, so each remained only moderately reactivated. In future work, we hope to test this by using neural classifiers to track recall of specific competing memories (Belal et al., 2018; Cairney, Guttesen, El Marj, & Staresina, 2018).

4.1. Effects of reward

Under both learning conditions, high-reward information was remembered better than low-reward information. We had predicted that, in the CPL condition but not the SPL condition, TMR cues would trigger prioritized replay of high-reward memories over low-reward memories, resulting in cue-induced strengthening of high-reward memories and

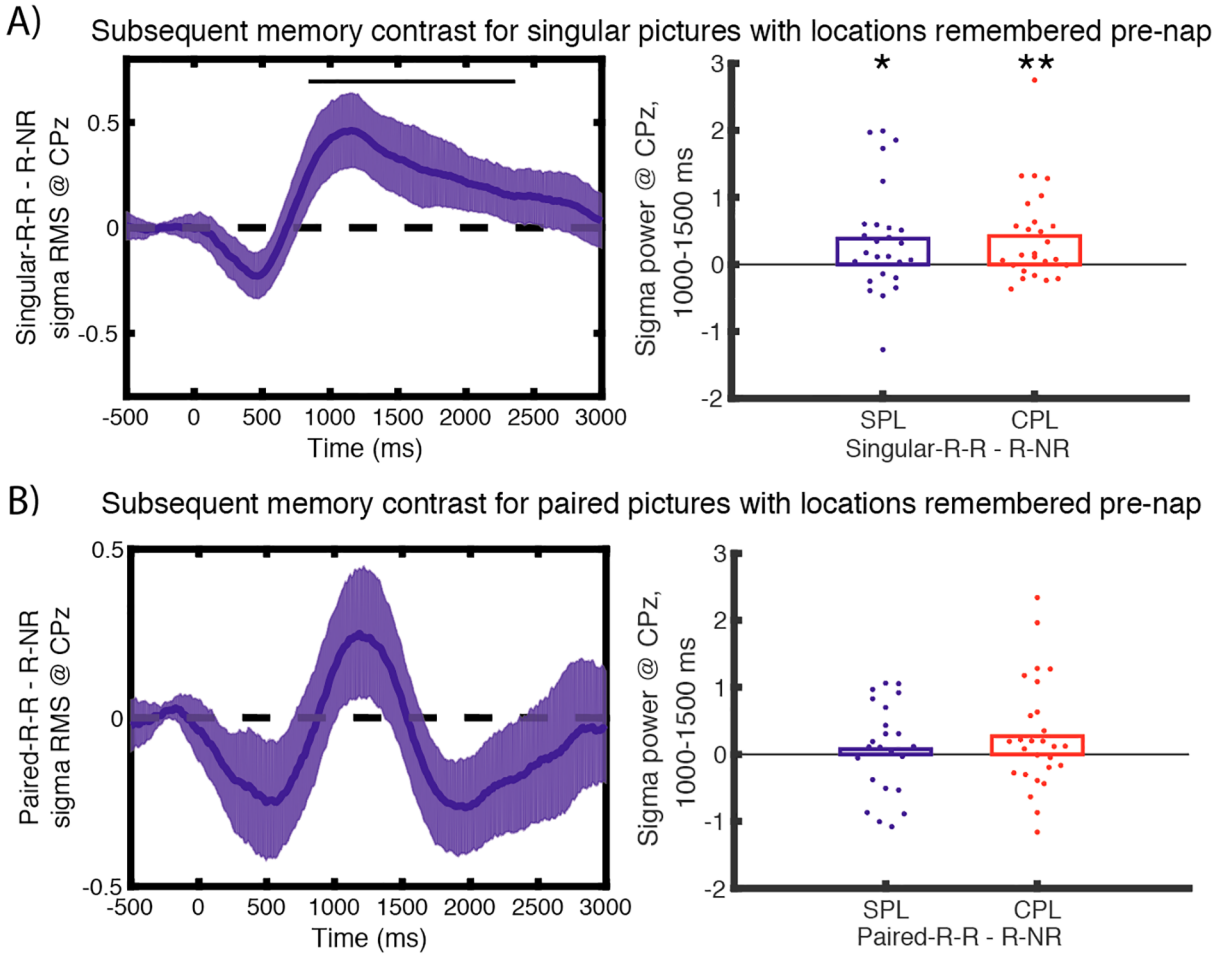

Fig. 6. Post-cue sigma power positively predicts subsequent memory, but not under high competition. Left plots show subsequent memory effects on sigma power for (A) singular pictures and (B) paired pictures whose locations were well-remembered pre-nap. Each plot shows a subtraction of the sigma power trace for pictures whose locations were remembered versus forgotten post-nap. Right plots show mean sigma power contrasts from 1000 to 1500 ms over CPz for each condition separately. Horizontal bars indicate time points that were significant at the $p < 0.05$ level. * indicates $p < 0.05$. ** indicates $p < 0.01$.

weakening of low-reward memories. However, the predicted three-way interaction between condition (CPL, SPL), cueing, and reward was not obtained, nor was there a two-way interaction between cueing and reward.

How can we explain the presence of a main effect of reward but the absence of an interaction between cueing and reward? Our prediction of an interaction was based on prior work suggesting that reward places a "priority tag" on memories, thereby boosting replay (Dunsmoor, Murty, Davachi, & Phelps, 2015; Gruber et al., 2016; Murty et al., 2017). One possibility is that participants differentially rehearsed high-reward picture-location pairs during wake (as we instructed them to do, by telling them to "maximize their score"), but participants did not attach enough value to these rewards to generate a "priority tag" that affected subsequent replay (after all, the rewards were quite small). Another possibility is that the reward manipulation was swamped by pre-experimental preferences. For example, pre-existing knowledge about or affective feelings towards Brad Pitt versus the Eiffel Tower (or the other well-known objects) could override the effects of rewards assigned to those pictures. Future studies that examine idiosyncratic preferences for or prior knowledge of each picture could provide further clarification. One additional possibility relates to the fact that our study used TMR, whereas the "prioritization" studies cited above examined spontaneous replay – it is possible that priority tags have a larger biasing effect on spontaneous replay than on cued replay.

4.2. Physiological effects: Beta and competition

Our EEG results align well with a recent model proposing that waking beta power (along with alpha power) plays a crucial role in memory encoding and adjudicating between competing memories at retrieval (Hanslmayr et al., 2012). Hanslmayr et al. (2009) found that higher beta power at encoding (during wake) predicted worse subsequent memory. Correspondingly, we found that spatial memory for singular and paired pictures in both learning conditions benefited from less beta power – this finding extends the Hanslmayr et al. (2009) result, showing that the negative relationship between beta and subsequent memory is also observed in response to TMR cues during sleep.

Furthermore, multiple studies have found increased beta power in conditions with greater competition. Waldhauser et al. (2012) found that beta power during wake increased with increased competition between items at retrieval and also predicted forgetting of the competing item. Also, Oyarzún et al. (2017) ran a TMR study relating beta to competition. In this study, participants learned the locations of two identical objects (X1-X2 learning) before learning a new location for one of the two objects (X1-X3), followed by sleep and the implementation of TMR. Like our study, this study created a situation in which TMR cues could elicit competition between memories (X1-X2 vs. X1-X3). X1-X3 learning occurred either shortly after X1-X2 learning (5 min) or after a longer delay (3 h). Intriguingly, the investigators

found that TMR improved memory for X1-X2 pairs in the former, short-delay condition and impaired memory when interfering learning occurred with a longer delay. They also found that beta power increased for TMR cues relative to control cues (sounds not linked to studied items), but only in the delayed-interference condition that showed the negative effect of cueing.

Based on these results, we predicted that beta power would be lower for cues linked to singular pictures (where competition is relatively low) vs. paired pictures (where competition is higher). This prediction was upheld. We also predicted that beta power would be larger for cues linked to paired pictures in the CPL (vs. SPL) condition – this prediction was *not* upheld. Reconciling the presence of behavioral differences in cueing effects for CPL vs. SPL with the lack of neural differences (both in beta power and in theta power) is an important question for future work. This null result suggests that EEG beta power differences may not pick up all relevant forms of competition. We speculate that the behavioral differences between competitive learning conditions could be reflected in hippocampal or other medial temporal neuronal firing patterns that are not readily detectable in scalp EEG. It is also possible that finer-grained measures of reactivation (e.g., using a classifier) would detect neural differences between CPL and SPL.

4.3. Physiological effects: Sigma

The role of sleep spindles in memory has received support from a vast array of research domains (Antony, Gobel, O'Hare, Reber, & Paller, 2012; Bergmann, Mölle, Diedrichs, Born, & Siebner, 2012; Eschenko, Mölle, Born, & Sara, 2006; Latchoumane, Ngo, Born, & Shin, 2017; Mednick et al., 2013; Niknazar, Krishnan, Bazhenov, & Mednick, 2015; Rosanova and Ulrich, 2005). TMR studies have repeatedly shown that sigma power approximately 1000–1500 ms post-cue, which might serve as a proxy for spindle activity (though might be different in some ways), positively predicts memory (Antony et al., 2018; Farthouat et al., 2017; Groch et al., 2017; Lehmann et al., 2016; Schreiner, Lehmann et al., 2015). Our data from singular pictures replicated these findings in both competition conditions. A similar, though nonsignificant, difference was observed for paired pictures in both conditions. These results provide further substantiation that post-cue spindle activity benefits memory. Further analyses of these spindle effects could potentially shed light on the physiological mechanisms of memory reactivation and consolidation.

4.4. Caveats and open questions

Importantly, while we observed robust differences in TMR effects following CPL versus SPL, we cannot pin down exactly which of the procedural differences between CPL and SPL were responsible for the differing results. One salient difference between the conditions is temporal proximity (paired pictures were studied one immediately after the other in CPL, whereas they were separated by a delay in SPL). However, Oyarzún et al. (2017) found negative effects of TMR when paired item-location memories were studied 3 h apart, indicating that close temporal proximity is not necessary to see negative effects of TMR. Another possibility is that our use of a competitive-rehearsal procedure (where participants were instructed to prioritize one picture location over the other picture location in the pair) was important for giving rise to the TMR-induced forgetting effects that we observed in CPL; it is possible that results could differ if participants were asked to integrate, rather than prioritize, the picture locations (Richter et al., 2016). Another difference between CPL and SPL is that each picture in the former condition was studied in succession with the same pairmate, whereas a given picture in the SPL condition was studied in succession with a variety of other pictures (each linked to a different sound). If SPL also used consistent pairings (e.g., meow + Brad Pitt was always rehearsed after violin + globe), this might create competition between these memories during sleep, even if the sounds were different. Future studies could include such alternative conditions to disambiguate these possibilities.

In addition to explaining why CPL leads to *greater* competition than SPL, we also need to explain how SPL avoids destructive competition effects in response to TMR cues. One important clue comes from the within-pair analyses that we ran in the SPL condition: We found that spatial memory for both high-reward and low-reward pictures benefited from TMR *on average*, but *within* a given pair either spatial memory for one picture or the other benefited from the cue, not both. This suggests that, in SPL, a single memory from the pair is "sampled" (Bornstein and Norman, 2017), thereby avoiding simultaneous activation and destructive competition. It is possible that this kind of sampling is the norm in memory retrieval, except in situations where memories have been entangled, e.g., by our CPL manipulation. Selective sampling may also help to explain the finding that TMR cues benefit memory when linked with an entire learning context, rather than specific trials (Diekelmann, Büchel, Born, & Rasch, 2011; Rasch et al., 2007; Rihm et al., 2014). Speculatively, presenting cues linked to an entire context may cause memories to be sampled individually in sequence, rather than simultaneously (Bornstein and Norman, 2017; Raaijmakers and Shiffrin, 1981); testing this is a topic for future investigation.

5. Summary

Our study demonstrated systematic differences in memory consolidation during sleep as a function of competition during learning. By pairing sound cues with more than one stimulus and then manipulating competition between these paired stimuli, our design produced new insights into memory consolidation during sleep. The findings support and extend previous evidence on beta and sigma power, which hold promise for continuing efforts to decipher the neurophysiology of memory processing. The study also expands the scope of memory processing that can be examined during sleep, beyond individual memories, here emphasizing inter-item competition. Although the physiology of sleep and wake differ substantially from each other, including the near-complete absence of cognitive control in the former, the results are consistent with those during wake showing that competition between two memories results in weakening (Lewis-Peacock and Norman, 2014).

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Conflicts of interest

The authors declare no competing financial interests.

Contributions

J.W.A., K.A.P., & K.A.N. conceived the design. J.W.A., L.Y.C., & P.P.B. collected the data. J.W.A., K.A.P., and K.A.N. analyzed the data. J.W.A., K.A.P., & K.A.N. wrote the manuscript. All authors discussed the results and revised the paper.

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