Respiration shapes the neural dynamics of successful remembering in humans.

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Abstract

Respiration has been shown to impact memory retrieval, yet the neural dynamics underlying this effect remain unclear. Here, we investigated how respiration shapes both behavioral and neural expressions of memory retrieval by re-analyzing an existing dataset where scalp electroencephalography and respiration recordings were acquired while participants (N = 18) performed an episodic memory task. Our results unveil that respiration influences retrieval-related power fluctuations in the α/β band and concomitant memory reactivation. Specifically, we found that both key neural signatures of successful remembering were co-modulated during exhalation, with the strength of the interaction between respiration and reactivation processes being associated with memory performance. Together, these findings suggest that respiration may act as a scaffold for episodic memory retrieval in humans by coordinating the neural conditions that support effective remembering.

Introduction

Compelling evidence from both rodent and human studies demonstrates that breathing might serve a purpose beyond supplying oxygen; it shapes neural activity during wake[1,2] and sleep[3,4]. Breathing-locked neural oscillations have been observed across diverse brain areas, oscillatory frequencies, and species[5–9]. While the precise mechanisms enabling this modulation remain unclear, evidence suggests that mechanoreceptors in olfactory sensory neurons, which respond to airflow, generate respiration-locked oscillations in the olfactory bulb[9–12]. These oscillations propagate along the olfactory pathway via the piriform and entorhinal cortices to neocortical and hippocampal regions[1,3]. However, since respiratory rhythm generators in the brainstem may also contribute to the entrainment of breathing-related neural oscillations[3,13–15], the preferred pathway through which breathing modulates neural activity remains uncertain.

Nevertheless, respiration has been shown - potentially through its impact on neural activity - to influence perceptual[16], motor[17,18], and cognitive processes[19] in humans. Performance is typically enhanced when stimuli are presented during inhalation[19–22], suggesting that inhalation-linked neural processes may aid perception. In contrast, mental actions such as motor and visual imagery tend to occur during exhalation[18], indicating that different phases of respiration may create time windows of opportunity for distinct cognitive functions[9]. Notably, memory processes have also been shown to be affected by the phase of respiration[23]. It has been demonstrated that retrieval-related reminder cues are more likely to trigger successful remembering if presented during inhalation as compared to exhalation[20], potentially due to stimulus processing being facilitated during inhalation. However, it is unknown whether memory-related neural processes, aside from stimulus-driven effects, might be associated with respiration, particularly during later phases of the breathing cycle, such as exhalation. Altogether, the results reported above suggest that respiration, and specifically its phase, may directly influence our ability to remember. But how could respiration facilitate effective memory retrieval?

In humans, memory retrieval has long been associated with characteristic patterns of neural activity. For instance, low-frequency power decreases in the α/β range (~8 – 30 Hz) have been consistently found to accompany successful remembering in

cortical areas and the hippocampus[24–27]. The magnitude of those decreases has been proposed to reflect heightened levels of information processing and retrieval-related engagement of cortical modules[25]. In line with this assumption, it has been shown that α/β power fluctuations do not only track the quantity but also the level of detail of memory-related information represented in the brain[28–30]. Moreover, several studies have established a tight link between α/β power decreases and the emergence of retrieval-related memory reactivation[31,32]. Specifically, retrieved memory information seems to be particularly decodable from electroencephalographic (EEG) signals during low α/β power levels[28,33], while other studies indicated that the low frequency oscillatory phase itself might carry a temporal signature of the reactivated memory content[34,35]. Importantly, beyond its close relationship with memory processes, α/β activity has been demonstrated to be robustly modulated by respiration during diverse cognitive tasks (i.e., visuospatial, lexical, and math)[19], perception[16] and rest[6]. Hence, respiration might accomplish its influence on the behavioral aspects of memory retrieval by modulating low-frequency oscillatory activity accordingly. However, it remains unknown whether and to what extent respiration might indeed coordinate retrieval-related power decreases in the α/β band and memory reactivation.

Here, we set out to directly assess the influence of respiration on the behavioral and neural expressions of memory retrieval using electroencephalography (EEG) and respiration recordings acquired during an episodic memory task. First, we replicate previous findings indicating that the phase of respiration at cue presentation influences memory performance, with successful retrieval being more likely when reminder cues were presented close to inhalation. We further show that this effect is potentially driven by respiration's impact on both power modulations in the α/β band and concomitant memory reactivation. Moreover, the strength of the interplay between respiration and retrieval-related reactivation is directly associated with behavioral memory performance. Our results identify respiration as a potential pacemaker for episodic memory retrieval in humans and pave the way for future research on brain-body interactions during memory formation.

Results

To examine whether respiration affects the behavioral and neural dynamics of memory retrieval, we analyzed EEG and respiratory recordings from 18 participants across two experimental sessions, each involving an episodic memory task (Fig. 1a). During the learning phase, participants were instructed to associate verbs with images of either objects or scenes, depending on the experimental session. Memory performance was evaluated in a sequential manner. Participants first completed a word-recognition task, classifying words (presented 3 s each) as "old" or "new." For words recognized as "old", participants attempted to retrieve the specific associated image (object or scene). Associative retrieval performance was normalized by the number of accurately recognized items ("hits"). Each session concluded with an independent "localizer task", during which participants were presented with a new set of stimuli comprising both object and scene images. The data of the localizer task were used to train a linear classifier in order to distinguish object- and scene-related EEG patterns during memory retrieval. Note that parts of the data have already been published, showing that (i) slow oscillation-spindle complexes clock memory reactivation during NREM sleep[36] and (ii) the occurrence of these sleep-related oscillations is modulated by respiration[4].

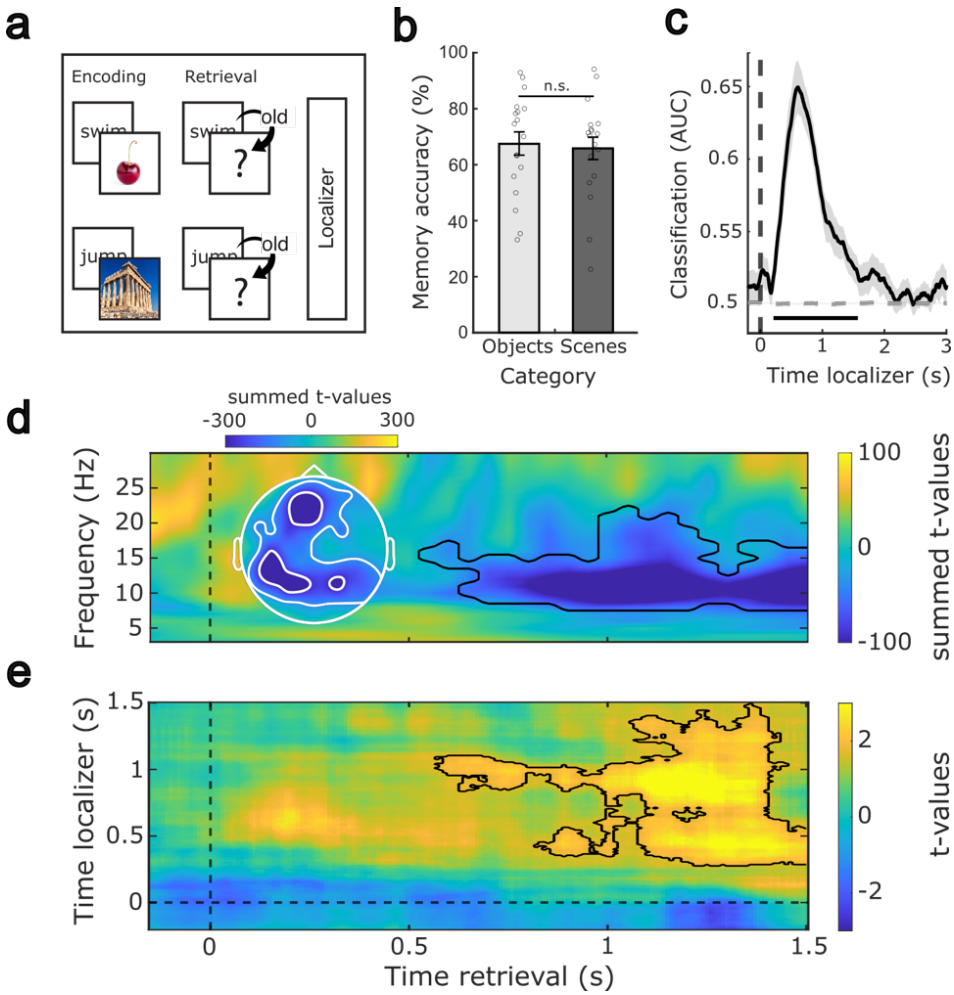

Figure 1. Experimental procedure, behavioral results, and retrieval-related EEG results. **(a)** During encoding, participants were presented with 120 verb-object or verb-scene pairs, depending on the experimental session, and memory performance was evaluated afterward. At the end of each session, participants performed a localizer task that involved processing a new set of object and scene images. **(b)** Behavioral results for both experimental sessions: objects (light gray) and scenes (dark gray). Bar graphs show the mean percentage (±SEM) of recalled image exemplars out of correctly recognized verbs. Dots indicate individual memory performance of participants (N = 18). No significant difference was found in memory accuracy between experimental sessions. **(c)** Stimulus categories (objects vs. scenes) could be decoded above chance from the localizer EEG data, starting around 150 ms post stimulus onset (the black solid line indicates decoding performance (±SEM)). The horizontal dashed line indicates surrogate decoding performance, which was estimated by shuffling the training labels 250 times. The vertical dashed line indicates stimulus onset (time = 0 s). The lower horizontal dark gray line shows the temporal extent of significant decoding results as derived from a dependent-samples t-test (one-sided, $p < 0.001$, corrected across time). **(d)** Remembered trials were associated with stronger power decreases in the α/β band (~8-20 Hz) after cue onset (~0.5 to 1.5 s) as compared to not remembered trials (contour lines indicate the extent of the significant cluster, $p < 0.001$; corrected across time, frequency and electrodes). The topographical inset illustrates the sum of t-values across all significant time points and frequencies for each electrode, illustrating that power differences were most prominent across frontal and parietal areas. **(e)** Learning-related brain patterns (objects vs. scenes) were decodable during retrieval (contour lines indicate the extent of the significant cluster, $p = 0.03$, one-sided; corrected across times); color range (blue to yellow) represents t-values comparing the decoding performance distributions of remembered versus not-remembered trials.

Behavioral results and localizer-related classification

As previously reported[36], memory performance was tested before and after a 120-minute nap (see Methods). To examine potential differences between the two learning categories (objects vs. scenes), memory scores were averaged across pre- and post-sleep sessions. No significant difference emerged between object and scene conditions (two-sided paired-sample t-test, $t_{(17)} = 0.37$, $p = 0.71$), suggesting that task difficulty was well matched across image categories (see Supplementary Table 1 for a detailed overview of memory measures). To derive the neural signatures of category-specific processing, which were used to track memory reactivation during retrieval, we employed a localizer task at the end of each session. During this task, participants viewed a novel set of images comprising both objects and scenes. Category-specific EEG patterns were extracted by aggregating the localizer data across experimental sessions and performing multivariate classification using linear discriminant analysis (LDA). Applying fivefold cross-validation, classification accuracy significantly exceeded chance levels between ~150 ms and 1500 ms after stimulus onset ($p < 0.001$, corrected across time, Figure 1c), indicating that the classifier reliably captured category-specific neural patterns of object and scene image processing.

Memory retrieval is associated with α/β power decreases and memory reactivation

As a first step, we set out to identify the oscillatory fingerprint of successful memory retrieval. To extract memory-related EEG patterns, we contrasted time-frequency representations between remembered and not-remembered items, based on associative memory test performance. In line with previous findings[24,29,37], successful remembering was associated with significant power decreases in the α/β range (~8 – 20 Hz), starting approximately 500 ms after cue onset across fronto-parietal areas ($p < 0.001$, corrected across time, frequency, and space; see Figure 1d). Next, we assessed whether neuronal activity related to the session-specific learning categories would be reactivated during successful retrieval[27,38]. Again, we trained an LDA classifier on the concatenated localizer data from both experimental sessions (objects and scenes; −0.15 to 1.5 s). The resulting training weights were then applied to retrieval data from both sessions, centered around cue onset (-0.15 to 1.5 s). The classifier testing labels matched the

stimulus category from the preceding encoding session (object or scene), such that above-chance classification reflects activation patterns that more closely resemble the newly learned stimulus category than the alternative one. As shown in Figure 1e, results revealed significantly higher classification performance for remembered as compared to not-remembered items emerging between 0.5 and 1.5 s relative to cue onset ($p = 0.03$, corrected across times).

Respiration phase modulates memory performance and EEG activity during retrieval

To assess whether the phase of respiration (mean respiratory frequency = 0.267 ± 0.041 Hz; for individual mean frequencies, see Supplementary Table 2) would impact memory performance during retrieval[20], cue-centered trials (-0.5 to 3 s; see Supplementary Fig. 1 for the cue-centered respiratory event-related potential) were segmented into 250 ms bins. Each bin was then categorized according to its proximity to either an inhalation peak (i.e., the inhalation-to-exhalation transition) or an exhalation trough (i.e., the exhalation-to-inhalation transition). Memory accuracy for both categories was computed within each time bin and normalized by the participant's individual overall performance. This yielded two time series per participant—one for bins aligned with the inhalation peak and one with the exhalation trough—capturing how changes in the respiratory phase over time impacted memory accuracy. A non-parametric cluster-based permutation test revealed that respiration significantly influenced retrieval performance (Fig. 2a). Specifically, successful retrieval was more likely in trials where the respiration cycle was closer to inhalation peaks between 0.125 and 0.625 s ($p = 0.047$, corrected across time) and to exhalation troughs between 1.875 and 2.375 s relative to cue onset ($p = 0.044$, corrected across time). Given the cyclical nature of respiration—moving from inhalation to exhalation—these findings suggest that trials in which participants inhaled around cue presentation and then transitioned to exhalation (within a trial) were more likely to be remembered.

To further corroborate this assumption, we divided the trials into two groups: one where inhalation peaks occurred before exhalation troughs during retrieval time and another where the order was reversed. Next, memory accuracy was computed for each of the categories. As shown in Fig. 2b, memory performance during retrieval was

194 significantly enhanced when inhalation peaks preceded exhalation troughs rather than
195 the other way around (dependent samples t-test, two-sided, $t_{(17)} = 2.87$, $p = 0.011$).
196 To examine whether respiration would likewise modulate EEG activity during
197 retrieval, we calculated the modulation index (MI)[39] to estimate cross-frequency phase-
198 amplitude coupling between respiration (providing the phase) and EEG signals across
199 all electrodes (providing amplitude measures between 3–30 Hz). For statistical
200 assessment, we generated an MI-level reference distribution by randomly shifting the
201 phase-related time series of each trial 200 times. The mean and standard deviation
202 across the reference distribution were then used to z-score the MI of the empirical
203 distribution. Results revealed a significant modulation of EEG amplitudes by the phase
204 of respiration with local peaks in the α (9 Hz, $z > 2.58$ / $p < 0.01$) and β range
205 (18 Hz, $z > 1.96$ / $p < 0.05$; Fig. 2c). Next, to specifically characterize EEG fluctuations in
206 the α/β band across the respiratory cycle, we divided the respiratory phase of each trial
207 into 60 evenly spaced bins (bin size = 6°). Then, the mean power in the α/β band (i.e., 8–
208 20 Hz, selected based on its association with successful memory retrieval, see Fig. 1d)
209 was computed for each phase bin across all trials and contrasted against a null
210 distribution (see Methods). We found respiration-locked EEG power exhibited
211 significant decreases around the exhalation through (114 to 138°, $p = 0.02$; 210 to 246°,
212 $p = 0.02$) and towards the inhalation peak (288 to 330°, $p < 0.01$; all corrected for multiple
213 comparisons across phase bins and electrodes, see Fig. 2d).
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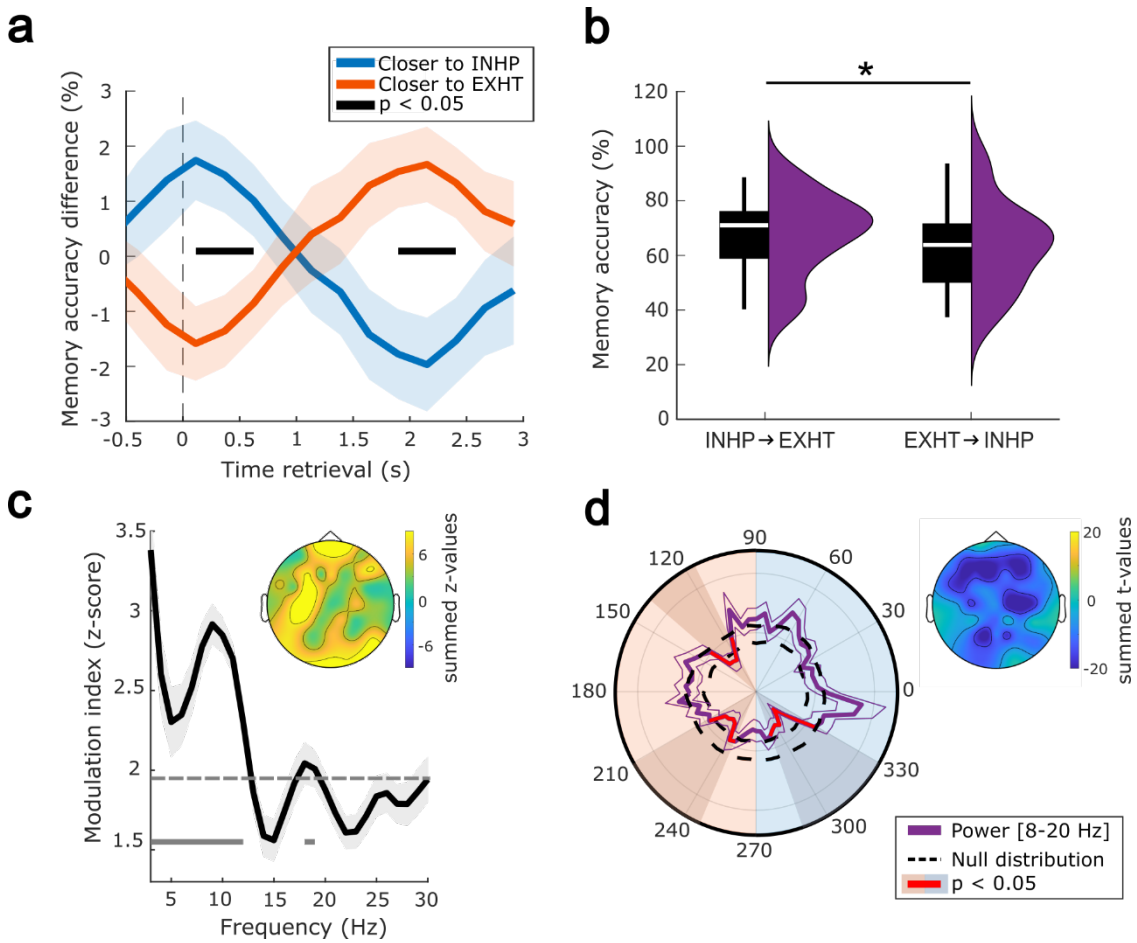

Figure 2. Respiration's impact on memory performance and oscillatory EEG activity. (a) Successful retrieval was more likely in trials where participants inhaled during the period of cue presentation—with inhalation peaks occurring between 0.125 and 0.625 s (p = 0.047, corrected across time)—and subsequently exhaled — with exhalation troughs occurring between 1.875 and 2.375 s (p = 0.044, corrected across time). Blue / orange lines represent the difference in accuracy with respect to the participant's overall memory performance for the trials that were closer to the inhalation peak /exhalation trough in each time bin (±SEM). The horizontal black line illustrates the temporal extent of significance as derived from a dependent-samples t-test (two-sided, cluster corrected across time). **(b)** Memory performance during retrieval was significantly enhanced when inhalation peaks preceded exhalation troughs rather than the other way around. Box plots show median (±$Q_{1/3}$) accuracy of recalled image exemplars out of correctly recognized verbs. Star denotes a significant difference as derived from a two-sided, dependent-samples t-test ($t_{(17)}$ = 2.8683, p = 0.0107). **(c)** The modulation index (± SEM, in shade grey) suggests that the phase of respiration significantly influences EEG amplitudes in the α/β range with local peaks at 9 Hz (z > 2.58) and 18 Hz (z > 1.96). The lower horizontal dark gray line depicts all significantly modulated frequencies, and the dashed line represents the threshold z value of significance (z = 1.96, p = 0.05). **(d)** Power in the α/β band is modulated at different phases of the respiratory cycle (purple solid line represents the power of [8-20 Hz] band (±SEM)). Segments in red indicate phase bins associated with significant power decreases in the α/β range as derived from a dependent-samples t-test against a shuffled reference distribution (114 to 138°, p = 0.02; 210 to 246°, p = 0.02; 288 to 330°, p < 0.01; two-sided, cluster corrected across phase and electrodes; inhalation peak = 0°). Light blue (orange) background represents phases closer to the inhalation peak (exhalation trough), with grey-shaded areas indicating significant phase bins. The topographical insert illustrates the sum of t-values across all significant phases for each electrode, showing that this decrease was more prominent in frontal, parietal, and right-central cortices.

Respiration modulates retrieval-related memory reactivation and its interplay with α/β power

Having established that respiration modulates both retrieval-related memory performance and EEG activity in the α/β range during retrieval, we finally asked whether respiration would also impact the emergence of memory reactivation. To this end, we detected exhalation troughs — the most prominent feature of the cue-locked respiratory ERP (see Supplementary Fig. 1)— in the respiratory signal during retrieval (0 to 3 s relative to cue onset) and centered the EEG data accordingly. Again, a classifier was trained on the pooled localizer data from both learning sessions (− 0.15 to 1.5 s), but the resulting training weights were this time specifically applied to the exhalation trough-locked EEG segments (±2 s, accounting for a whole respiratory cycle with a mean respiratory frequency of 0.25 Hz). Results revealed significantly higher decoding performance for remembered as compared to not-remembered trials emerging just prior to the exhalation through ($p = 0.04$, corrected across times, Fig. 3a).

To further assess the functional significance of the coupling between memory reactivation and respiration, we determined its impact on the participants' memory performance. To this end, we extracted decision values from the decoding procedure, yielding a single-trial, time-resolved metric that reflects the classifier's confidence in assigning a specific category (objects vs. scenes) in the cue-centered EEG data (see Supplementary Fig. 2)[40]. Then, for each of the remembered trials, we extracted the respiratory phase where decision values reached their maximum. We found that decision value maxima consistently emerged during exhalation across participants (mean angle = 93.045° ± 0.321; Rayleigh test $z = 14.58$, $p < 0.001$; see polar insert in Fig. 3b). Finally, when correlating the vector length (representing the coupling strength between respiration and classification maxima across trials) with memory performance, we observed a significant positive relationship (Fig. 3b; Spearman's Rank Correlation, $r = 0.558$, $p = 0.018$; for results based on non-remembered trials see Supplementary Fig. 3). The distribution indicated that the stronger the reactivation-related EEG signatures were modulated by respiration, the better the memory performance.

So far, we have demonstrated that respiration might serve as a temporal anchor for retrieval-related neural processes, as both characteristic power decreases in the α/β

band and memory reactivation were significantly modulated by the phase of respiration. Hence, we hypothesized that respiration might co-modulate both key markers of successful memory retrieval. Thus, we extracted trial-based decision values, locked to exhalation troughs, and correlated them with α/β power values at each electrode and timepoint across trials. When contrasting correlational values between remembered and not-remembered trials, we observed a significant negative cluster emerging just prior to the exhalation through (p = 0.023; corrected for multiple comparisons across time and electrodes, Fig. 3c), indicating that the stronger the respiration locked α/β power decrease, the higher the classifiers fidelity during successful remembering.

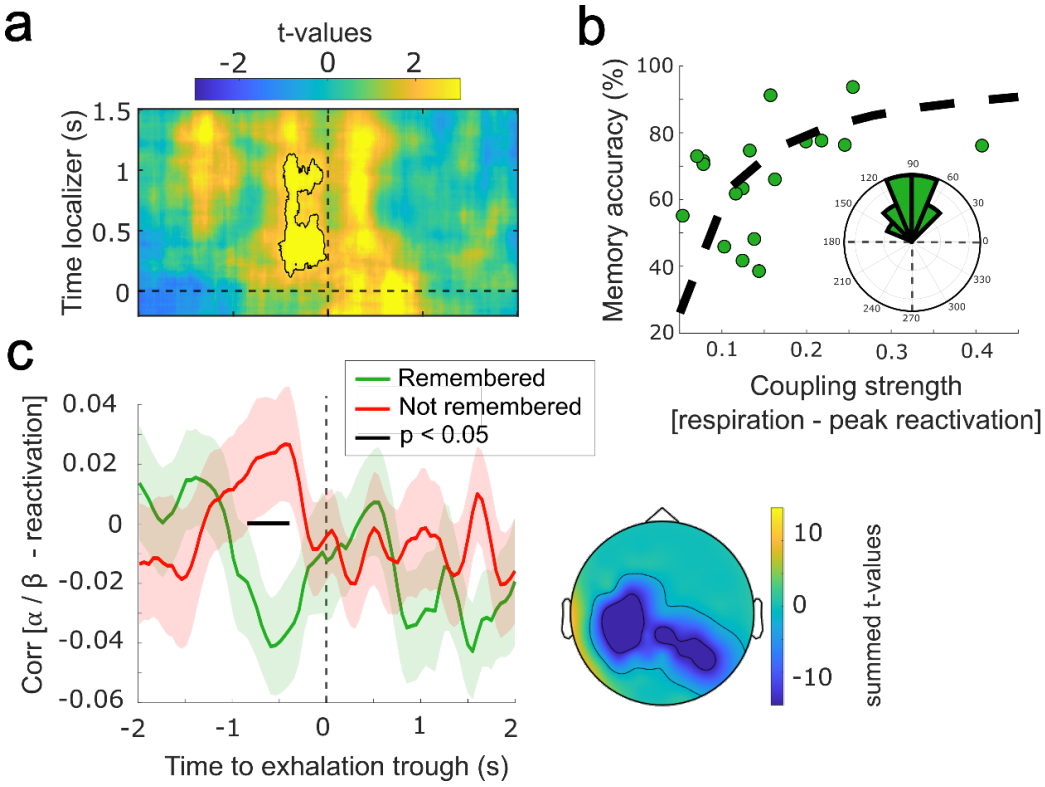

Figure 3. Respiration impacts memory reactivation and concomitant α/β power fluctuations. (a) Learning-related brain patterns (objects vs. scenes) were decodable during retrieval **based on** exhalation trough-centered EEG data (contour lines indicate the extent of the significant cluster, p = 0.04, one-sided, corrected across times; color range (blue to yellow) represents t-values of remembered against not-remembered distributions of decoding performances). **(b)** In remembered trials, coupling strength (measured as vector length) between respiration and classification maxima is positively correlated with memory performance (Spearman's Rank Correlation, r = 0.558, p = 0.018). Nonlinear fit as a dashed black line (only for visualization purposes). The polar histogram illustrates the mean respiratory phase at which decoding-derived reactivation peaks emerge during remembered trials for each participant (mean angle = 93.045° ± 0.321; Rayleigh test z = 14.58, p < 0.001; inhalation peak = 0°). **(c)** Decoding-derived single trial decision values and α/β power (8-20 Hz) are more negatively correlated prior to the exhalation trough in remembered trials as compared to not-remembered trials. The green (red) solid line shows the Spearman's correlation for (not) remembered trials (±SEM). The horizontal black line shows the temporal extent of significant results as derived from a dependent-samples t-test (two-sided, p = 0.023, cluster corrected across time and electrodes). The topographical inset illustrates the sum of t-values across all significant timepoints for each electrode, showing that this difference was stronger in the parietal cortex.

Discussion

Our results unveil a role of respiration in modulating both behavioral and neural components of successful remembering. In line with previous research, we show that the phase of respiration influences memory performance (Fig. 2a), with successful retrieval being more likely when reminder cues were presented close to inhalation. Moreover, key neural signatures of successful remembering – oscillatory power decreases in α/β band (Fig. 2d) and memory reactivation (Fig. 3a) – as well as their interplay (Fig. 3c) were modulated by respiration. Finally, the strength of the coupling between respiration and reactivation processes was associated with memory performance (Fig. 2b), underscoring the functional relevance of respiration–brain interactions for memory.

Extensive research in both rodents[3,11,41] and humans[2,6,20] indicates that respiration might be essential for modulating neural oscillations across various brain regions and frequency bands. Mechanistically, it has been suggested that the impact of respiration on neural activity is mediated by incoming airflow stimulating mechanoreceptors in olfactory sensory neurons[12]. Through this stimulation, breathing-locked oscillations are generated and then relayed to the olfactory cortex and spread to various target regions[9,10,12]. However, respiration has also been shown to impact cognition in various domains such as motor control[17,18], perception[16,42] , and emotion[21], often enhancing performance when stimuli are presented during inhalation[7]. In particular, a growing number of findings in humans demonstrate that breathing impacts memory processes during wake[23 (but see 43,44)]. Zelano and colleagues were the first to show that during retrieval testing, memory was better for stimuli that were presented during inhalation as compared to exhalation[20]. Interestingly, this effect became only evident when participants engaged in nasal breathing (as compared to mouth breathing), suggesting a specific role for nasal respiration in orchestrating memory-related processes. Our data remain agnostic as to whether nasal breathing is indeed crucial for impacting memory performance. Nevertheless, our finding that successful retrieval was more likely when participants inhaled during reminder cue presentation is in line with the previous result, indicating that the phase of respiration at the time of cue presentation impacts memory performance. However, while these results appear to suggest that stimulus processing

might be facilitated during inhalation, the neural mechanisms underlying respiration's influence on successful memory retrieval have remained unexplored.

Cortical power decreases in the α/β band have consistently been reported to index successful memory retrieval[24–27]. It has been suggested that these decreases might facilitate remembering by allowing neural assemblies to express the specific neural codes associated with stored memories[25 (but see 45)]. Indeed, α/β power modulations have been shown to track the amount and content of information being retrieved[25,46,47], the fidelity of memory details[28–30], and potentially provide time-windows of opportunity for memory reactivation[24,35,48]. Also, in our data, successful retrieval, irrespective of respiration, was associated with robust power decreases in the α/β band across frontal and parietal areas. Moreover, implementing two learning sessions per participant, each utilizing distinct and analytically distinguishable learning stimuli (object and scene images, Fig. 1a), allowed us to track the emergence of retrieval-related memory reactivation and demonstrate that learning-related brain patterns were specifically decodable during periods of low α/β power.

Beyond these confirmatory findings concerning the role of low-frequency power decreases and concomitant memory reactivation in memory retrieval, our results suggest that respiration might play a crucial role in modulating those neural dynamics underlying successful remembering. Fluctuations in α/β activity have already been demonstrated to be influenced by respiration during diverse cognitive tasks (i.e., visuo-spatial, lexical, and math)[19], perception,[16] and rest[6]. Our results critically extend these findings by demonstrating that also retrieval-related α/β fluctuations are tightly modulated by respiration. Specifically, we found that decreases in α/β activity systematically emerged both around exhalation troughs and just prior to inhalation peaks. These power reductions, synchronized with different phases of the respiratory cycle, may serve distinct functional roles. As outlined above, our behavioral analyses revealed that successful remembering was more likely when participants inhaled during the reminder cue presentation and exhaled thereafter (i.e., with exhalation troughs occurring between 1.875 and 2.375 s after cue onset). Interestingly, in addition to their role in memory retrieval, low pre-stimulus α/β levels have consistently been linked to enhanced perceptual performance[49]. Thus, inhalation-locked decreases in low-frequency power

may facilitate stimulus perception[16], forming a fundamental foundation for cue-triggered remembering. On the contrary, signatures of retrieval-related memory reactivation are typically observed between ~500 and 1500 ms after reminder cue onset[38]. Accordingly, low-frequency power decreases emerging around exhalation troughs might establish a neural environment that is optimally tuned for memory reactivation to unfold. This interpretation is in line with our finding that not only power decreases in the α/β band were modulated by exhalation, but that classification-derived memory reactivation, hence the putative neural substrate of remembering[31], emerged just prior to the detected exhalation troughs. Therefore, our results add further evidence to the notion that that different phases of respiration might establish time windows of opportunity for distinct brain functions[9]. In addition, respiration has recently been established to similarly influence the emergence of sleep-related oscillations and in consequence, memory reactivation in humans[4], with reactivation processes putatively unfolding during exhalation. Together, these results suggest that respiration might impact memory-related neural oscillations and concomitant memory reactivation in a consistent manner, regardless of state.

The negative correlation between α/β power levels and memory reactivation signatures prior to exhalation troughs during memory retrieval suggests that respiration may influence the interplay between these two key markers of successful memory retrieval. However, it remains to be determined whether the emergence of memory reactivation is directly shaped by respiration or through its effect on α/β activity. Future research employing intracranial recordings may help resolve this uncertainty by examining whether respiration modulates the emergence of hippocampal ripples during retrieval[50]. Considering that ripples—integral to triggering memory reactivation in both hippocampal and cortical regions[51]— have been shown in rodent[3,52] and more recently in humans[53] to be modulated by respiration, particularly during exhalation, such investigations could provide crucial insights into whether respiration directly influences memory reactivation. In any case, our finding that the strength of the coupling between respiration and markers of memory reactivation predicts individual memory performance provides compelling evidence for the functional significance of this relationship (irrespective of a direct or indirect impact of respiration on reactivation processes).

To conclude, our results reveal a critical role for respiration in modulating both the behavioral and neural aspects of successful remembering. They identify respiration as a pacemaker for effective remembering and highlight the importance of brain-body interactions in human memory processing.

Methods

The current analyses are based on reference[36], where detailed information about participants, stimuli, task, and data acquisition can be found. The data of two participants (out of 20) had to be excluded due to low trial numbers (< 15 trials in any of the conditions). In summary, the study involved 18 healthy participants (mean age: 20.89 ± 0.34; 15 female). Pre-study screening, which included the Pittsburgh Sleep Quality Index (PSQI[54]), the morningness-eveningness questionnaire[55], and a custom questionnaire assessing general health and stimulant use, confirmed that participants were not taking any medication and had no neurological or psychiatric conditions at the time of the experiment. The University of Birmingham Research Ethics Committee approved the study, and all participants provided written informed consent. They were compensated either financially or with course credit for their participation.

Experiment overview

The experiment involved two sessions per participant, spaced at least one week apart (mean interval: 7.78 ± 0.43 days), with the session order counterbalanced across participants. On each experimental day, participants arrived at the sleep laboratory at 11 a.m., where the set-up for polysomnographic recordings began. Electrodes for electroencephalography (EEG), electromyography (EMG), and electrocardiography (ECG) were applied, along with a thermistor airflow sensor to monitor breathing. Around noon, the experiment commenced with a modified psychomotor vigilance task (PVT[56]), followed by a memory task (see Encoding and Memory tests below) in which participants learned to associate 120 verbs with images (either objects or scenes[57], depending on the session). The sleep period began at approximately 1 p.m., giving participants the opportunity to nap for ~120 minutes. After the nap, their vigilance was reassessed using the PVT, and memory performance was tested again. A localizer task was conducted at

the end of each session (see Localizer task below). Behavioral responses and the presentation of tasks were managed using Psychophysics Toolbox Version 3[58] and MATLAB 2018b (MathWorks, Natick, USA).

Stimuli. The experimental stimuli consisted of 360 verbs and 240 images, evenly divided between object and scene categories, presented during both experimental sessions. Object images depicted animals, food items, clothing, tools, or household items against a plain white background (e.g., a calculator). Scene images represented identifiable landscapes or locations (e.g., an island). These categories were chosen as they engage distinct brain networks, such as the lateral occipital complex for object processing[59] and the para-hippocampal place area for scene processing[60], facilitating the investigation of experience-driven memory reactivation during retrieval (see Methods: Multivariate analysis). All images were obtained from reference [57].

Familiarization. The experiment commenced with an image familiarization phase designed to (i) facilitate the learning of verb-image associations during the subsequent encoding session and (ii) establish accurate image labels for later cued recall. Each trial began with the presentation of a fixation cross for 1.5 ± 0.1 s. Participants were then shown one of 130 images depicting either objects or scenes, depending on the experimental session. Of these, 120 images were included in the learning material and accompanied by captions accurately naming the depicted exemplars. An additional 10 images, which were not used further in the experiment, were paired with incorrect captions. Each stimulus was displayed for 2.5 s. Participants were instructed to press a button upon detecting an erroneous image-caption pairing.

Encoding. Each trial began with the presentation of a fixation cross for 1.5 ± 0.1 s, followed by a verb (e.g., "jump") displayed for 1 s. Immediately after, the corresponding image to be associated with the verb was presented for 4 s. Participants were instructed to create a vivid mental image or narrative linking the verb with the object or scene depicted in the image. Following the image presentation, participants indicated whether the mental image they had formed was realistic or bizarre. Participants were informed in

advance that their memory for the verb-image pairs would be tested subsequently. The learning block was repeated twice with a randomized trial order in each iteration to achieve satisfactory memory performance, as established in a prior pilot study.

Memory tests. Participants' memory for the encoded verb-image pairs was assessed both before and after the nap interval. To mitigate potential testing effects on behavioral measures of memory consolidation[61,62], only half of the learned verb-image pairs were included in each memory task, with no overlap between the two tests. Each memory test comprised 60 randomly selected verbs from the learning phase, intermixed with 30 novel verbs ("foils") that had not been presented during learning. Each trial began with a fixation cross displayed for 1.5 ± 0.1 s, followed by the presentation of a verb on the screen. After 3 s, participants indicated within a 10 s window whether the verb was "old" (i.e., part of the learning material) or "new" (i.e., not seen during learning). For "new" responses, participants proceeded directly to the next trial. For "old" responses, participants were prompted to either type a description of the associated image or enter "do not know" if they could not recall the target image. Responses were scored as correct if (i) the typed description matched the original caption presented during the familiarization phase or (ii) the description unambiguously corresponded to the content of the target image.

Localizer task. During the localizer task, participants viewed a new set of images comprising 90 objects and 90 scenes, irrespective of the experimental session. Each trial began with a fixation cross presented for 1.5 ± 0.1 s, followed by the display of a randomly selected image (object or scene) on the computer screen for a duration between 2.5 and 10 s. Each image was presented twice during the task, and participants were instructed to indicate whether the image was being shown for the first time ("new") or the second time ("old").

EEG and respiration

A Brain Products 64-channel EEG system was used to record electroencephalography (EEG) throughout the experiment. Impedances were kept below 10 kΩ. EEG signals were

referenced online to electrode FCz and sampled at a rate of 1000 Hz. Respiration was recorded using an Embla thermistor airflow sensor.

Data analysis

Behavioral. Analysis was performed based on associative memory performance, calculated as the proportion of correctly remembered images relative to the number of 'hit' trials (i.e., verbs correctly identified as old), separately for each session (object and scene) and memory test (pre- and post- sleep). To relate the respiratory phase to memory performance across trials (Fig. 2a), we first collapsed all trials from both sessions and memory tests (i.e., pre- and post-sleep). Then, trials were segmented into 250 ms bins, starting -0.5 s before cue onset. For each time bin, we categorized trials based on whether the circular mean of the respiration phase across the 250 ms of a bin aligned more closely with the inhalation peak or the exhalation trough, respectively. Memory accuracy was then computed for each category (inhalation and exhalation relatedness, respectively) within each time bin and normalized by each participant's overall memory performance. Finally, to analyze whether specific respiration sequences (inhalation to exhalation or exhalation to inhalation) during retrieval influence memory performance, we categorized trials based on the presence of either an inhalation peak followed by an exhalation trough or the reverse within -0.5 to 3 s from cue onset. Then, associative memory performance was computed for each category.

EEG and respiration. All data were analyzed using MATLAB (2020a; MathWorks). EEG data were preprocessed using the FieldTrip toolbox[63] for EEG/MEG analysis (v.16/07/2023). All data were downsampled to 200 Hz and re-referenced using a common average reference (CAR). Noisy EEG channels were identified by visual inspection, discarded, and then interpolated using a weighted average of the neighboring channels. EEG epochs related to the retrieval task were locked to two different events: stimulus presentation and exhalation troughs. Exhalation troughs (and inhalation peaks for Fig. 2b) were detected using the Breathmetrics toolbox[64]. Trials were classified into remembered and not-remembered categories based on associative memory performance. In the case of localizer trials, all data were locked to the stimulus onset with

515 a temporal window of -0.2 to 3 s. For analyses related to respiratory phase, the phase
516 was extracted using the double interpolation method[4,16], unless specified otherwise.
517
518 Time-frequency analysis. Time-frequency analysis of stimuli-locked (-2 to 3 s) and
519 respiratory event-centered EEG segments (−5 to 5 s) was performed using FieldTrip[63].
520 The longer time segments were chosen to allow for resolving low-frequency activity
521 within the time windows of interest for both stimuli-locked (-0.2 to 1.5 s) and respiratory
522 event-locked (−2 to 2 s) and avoid edge artifacts. Frequency decomposition of the data
523 was achieved using Fourier analysis based on sliding time windows (moving forward in
524 50 ms increments). The window length was set to five cycles of a given frequency
525 (frequency range: 1–30 Hz in 1 Hz steps). The windowed data segments were multiplied
526 with a Hanning taper before Fourier analysis. Afterward, power values were z-scored
527 across time, using a 1 s baseline window prior to stimulus onset. To analyze oscillatory
528 power as a function of the respiratory phase, power values were transformed from the
529 time axis to the phase axis. For that, the respiratory cycle was divided into 60 non-
530 overlapping phase bins (bin size = 6°), and after assigning all power values to the
531 respiratory phase bin where they occurred, the mean power was computed for each
532 bin[16,65]. Thus, we obtained a respiratory phase-resolved distribution, with the value at
533 each phase bin representing the mean of all power values that overlapped with that
534 respiratory frequency across all trials from 0 to 3 s.
535
536 Modulation Index. Phase amplitude coupling was assessed using the Modulation Index
537 (MI)[39]. To estimate the instantaneous phase of the respiration signal, we filtered the
538 continuous respiratory data around the peak frequency of each particular subject (see
539 Supplementary Table 2) ± 0.05 Hz two-pass Butterworth band-pass filter). We then
540 extracted instantaneous amplitude data across frequencies between 3 and 30 Hz at each
541 electrode in steps of 2 Hz. To this end, a two-pass FIR filter (order = three times the lower
542 frequency bound) was used to create 27 equally spaced frequency bins, with center
543 frequencies ranging from 3 to 30 Hz, and with fixed-frequency bandwidths of 2 Hz. The
544 envelope of the Hilbert-transformed band-pass filtered data was then used as an
545 amplitude estimate. To compute the MI (for a given frequency pair), we divided the

phase signal into 20 bins, and then, for each bin, computed the mean amplitude. This yields a distribution of amplitude as a function of phase. The MI is defined as the Kullback–Leibler distance between that distribution and the uniform distribution (across the same number of bins). To assess the statistical significance of MI values, we randomly shifted the phase time series and computed the MI using the shifted signal. We repeated this procedure 200 times, resulting in a MI-level reference distribution. The mean and standard deviation across the reference distribution was then used to z- score the MI of the empirical data. Z values were then transformed into *p* values, with a significance threshold of z values greater or smaller than ±1.96.

Multivariate analysis. Multivariate classification of single-trial EEG data was performed using MVPA-Light, a MATLAB-based toolbox for multivariate pattern analysis[66]. For multivariate classification, Linear Discriminant Analysis (LDA) was used as classifier[66].

For multivariate classification of the localizer task EEG data, we downsampled (100 Hz) and then z-scored the localizer data across all trials independently for each time point. Data from both sessions were then combined and subjected to principal component analysis (PCA), which transforms the data into linearly uncorrelated components ranked by the variance explained by each component[67]. PCA was employed to reduce dimensionality and mitigate overfitting, retaining the first principal components that explained 95% of the data's variance[68]. To assess whether object and scene representations could be distinguished in the localizer, we trained and tested a classifier to discriminate between object and scene trials. A 200 ms running average smoothing window was applied to the data. EEG channels were treated as features, and a separate classifier was trained and tested at each time point. Classification performance was quantified using the area under the receiver operating characteristic curve (AUC), which measures the probability that a randomly selected pair of Class A and Class B trials is correctly assigned to their respective classes (0.5 = chance level; 1.0 = perfect classification). To prevent overfitting, fivefold cross-validation was implemented, with the analysis repeated five times to account for variability arising from random fold assignments[69]. The results were averaged across iterations. Statistical significance was evaluated by generating surrogate decoding performance values through 250 iterations

of label shuffling, producing baseline values under the null hypothesis of label exchangeability.

To investigate differential evidence for object vs. scene representations as a function of prior learning during the retrieval task, we used the temporal generalization method[70]. First, we applied the same preprocessing described above to the concatenated localizer and retrieval data. A classifier was trained at each time point in the localizer data and applied to each time point during retrieval, specifically for remembered and not-remembered trials. No cross-validation was required since localizer and retrieval datasets were independent. As a metric, we again used the AUC.

For trial-based analyses (Fig. 3b-c), decision values[40] were extracted at each time point in the localizer and retrieval phases for each individual trial of the retrieval task (cue-centered for Fig. 3b; exhalation trough-centered for Fig. 3c). These values were then averaged across the significant time window in the localizer (150 to 1500 ms), resulting in a trial-by-retrieval time matrix. The modulus of the decision values was used to represent the model's confidence at each time point of every trial, regardless of the trial's original category. For the analysis in Fig. 3b, the maximum decision value of each trial was calculated to obtain the respiratory phase at peak reactivation.

Statistics. Behavioral retrieval data were averaged across conditions (object- and scene-condition, pre- and post-sleep) and subjected to a two-sided dependent-sample t-test (Fig. 1b for category comparison). To examine the effect of the sequence order of respiratory events (Fig. 2b) on memory performance, a two-tailed paired-sample t-test was conducted. For correlation analyses, Spearman's correlation was used. To assess the relationship between oscillatory power (8 to 20 Hz) and memory reactivation (decision values) across exhalation trough-locked retrieval times, correlational values were smoothed using a 250 ms moving mean before statistical analysis.

All data were collapsed across both sessions (objects and scenes) and memory tasks (pre- and post-sleep) per participant before entering statistical analysis. Unless stated otherwise, we used non-parametric cluster-based permutation tests implemented in FieldTrip[63], which do not rely on the assumption of a specific underlying distribution. A dependent-samples t-test was conducted at the sample level to identify clusters of

contiguous time points across participants, with values thresholded at $p = 0.05$. The cluster statistic was defined as the maxsum (sum of all t-values within a cluster), and Monte Carlo simulations were performed to determine the cluster *p*-value (alpha = 0.05, two-tailed, unless the corresponding analysis can only yield meaningful unidirectional results (Fig. 1c, Fig. 1e and Fig. 3a)) based on the permutation distribution. For circular analyses, data were divided into 60 distinct phase bins (bin length = 6°), and mean values were calculated within each bin. To assess statistical significance, the time course values within each trial were shuffled across trials 1000 times per subject and electrode, maintaining the original respiration phase to create a null distribution for each participant. This conservative approach ensures that the temporal characteristics of the respiratory signal is preserved[71]. Significance was determined by non-parametric cluster-based permutation tests for circular data.

Declaration of interests

The authors declare no competing interests.

Data availability

All data supporting the findings of this study will be made publicly available upon publication.

Code availability

All code related to the analyses of the manuscript will be made publicly available upon publication.

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Contributions

T.Sc., M.P. and B.P.S. conceived the study and designed the experiment. T.Sc. conducted the experiment. E.B.T and T.Sc. analyzed the data. E.B.T., F.S, M.P., T.St., B.P.S. and T. Sc. wrote the paper.

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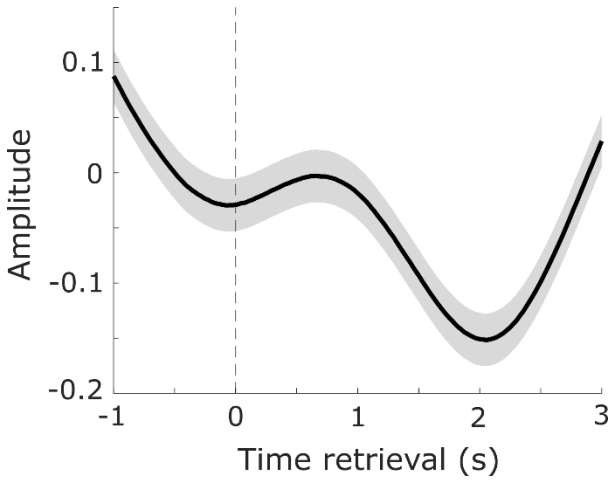
Supplemental Information

	Objects	Scenes	*t*	*p*
Recognition [Hits] %				
pre-sleep	74.14±3.97	73.80±4.15	0.12	0.90
post-sleep	64.54±3.98	66.05±4.45	-0.60	0.56
post- relative to pre-sleep	87.31±2.85	88.68±2.34	-0.39	0.70
Recognition [Correct Rejections] %				
pre-sleep	90.00±2.40	87.41±4.70	0.60	0.56
post-sleep	88.33±3.19	84.63±5.70	0.72	0.48
post- relative to pre-sleep	97.77±1.72	96.22±3.92	0.43	0.67
Associative Memory %				
pre-sleep	52.77±4.71	51.36±4.67	0.40	0.70
post-sleep	42.75±4.88	39.08±3.84	0.87	0.40
post- relative to pre-sleep	79.28±4.83	76.43±4.05	0.38	0.71
Associative Memory [out of hits] %				
pre-sleep	70.18±3.59	69.85±4.16	0.09	0.93
post-sleep	64.83±5.38	61.92±4.60	0.52	0.61
post- relative to pre-sleep	90.52±4.82	87.19±3.69	0.55	0.59

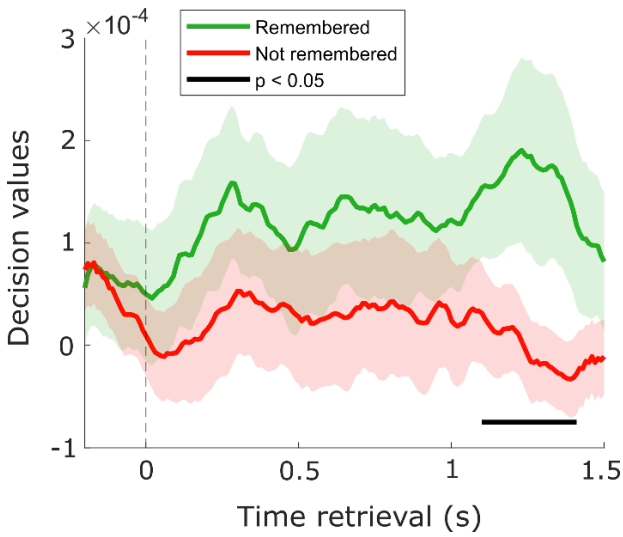
Supplementary Table 1. Overview of memory performance. Associative memory % refers to the percentage of correctly recalled images (relative to the total number of stimuli), while associative memory [out of hits] refers to the percentage of recalled image exemplars out of correctly recognized verbs. Statistical differences between conditions (objects vs. scenes) were assessed using dependent samples t-tests (two-sided).

PARTICIPANT	BREATHING FREQUENCY (HZ)
P02	0.3
P05	0.27
P07	0.185
P09	0.235
P11	0.23
P12	0.285
P13	0.285
P14	0.3
P15	0.28
P16	0.215
P19	0.35
P21	0.22
P22	0.27
P25	0.315
P26	0.27
P29	0.25
P30	0.3
P31	0.25
MEAN ALL (±SD)	0.2672 ± 0.0405

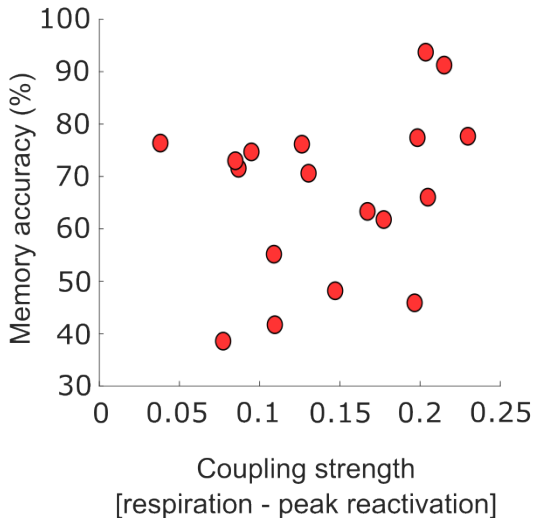
Supplementary Table 2. Mean breathing (± SEM) frequency of each participant.



Supplementary Figure 1. Grand everage (±SEM) of the respiratory signal locked to the cue onset (t = 0 s, dashed line). The respiratory signal was recorded with a thermistor. A positive slope indicates inhalation, whereas a negative slope reflects exhalation.



Supplementary Figure 2. Mean (± SEM) decision values from the output of the classification model for remembered (green) and non-remembered (red) trials, averaged over the period of significant localizer decodability (250 to 1500 ms). The lower horizontal black line shows the temporal extent of significant results as derived from a dependent-samples t-test (two-sided, cluster corrected across time). There is a significant increase in the model's confidence occuring between 1.10 and 1.41 s for remembered trials with respect to non-remembered ones (p = 0.041).



Supplementary Figure 3. Coupling strength (measured as vector length) between respiration and not remembered trials' maximum decision values from the LDA model (Spearman's Rank Correlation, r = 0.2816, *p* = 0.2577).