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Long-term memory retrieval bypasses working memory



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ABSTRACT

For decades, it has been assumed that when humans retrieve information from long-term memory (LTM), information need first to be brought back into working memory (WM). However, as WM capacity is limited, it is unclear what happens if information from LTM needs to be retrieved while WM is fully engaged? To address this question, observers had to retrieve colors from LTM while WM storage capacity was fully engaged. The behavioral results showed that retrieving information from LTM is possible even when WM capacity is fully occupied. Additional evidence from electroencephalogram (EEG) confirmed that WM was fully engaged as the suppression of alpha oscillation reached its maximum when memorizing the maximum amount of information into WM; yet the suppression in alpha oscillation was even further amplified when items were retrieved simultaneously from LTM, providing a neural signature of additional LTM retrieval capacity above and beyond the maximum WM capacity. Together, our findings indicate that information retrieved from LTM does not always have to be brought back into WM, but instead might be accessed through a different mechanism when WM is fully engaged.

Introduction

Human memory is generally considered to include two separate memory systems: Long-term memory (LTM) for storing a limitless amount of information (Brady et al., 2008, 2011) and Working memory (WM) for temporally storing a limited amount of information which is typically used for performing ongoing cognitive tasks (Baddeley and Hitch, 1974; Cowan, 2001). As has been shown in various behavioral studies (Cantor and Engle, 1993; Graesser and Mandler, 1978; Nairne and Neath, 2001), it is assumed that LTM information first needs to be retrieved into WM before it can be used to perform cognitive tasks (Atkinson and Shiffrin, 1968; Broadbent, 1975; James, 1890). Also, previous work has indicated that LTM retrieval involves WM, which is part of the reason why there are individual differences in WM capacity (Cowan et al., 2003).

Most recently, Fukuda and Woodman (2017) provided direct evidence for the role of WM in retrieving information from LTM. In two different tasks, they tracked information retrieved from LTM and compared that to the neural trace from WM in electroencephalogram (EEG) measures. In the encoding task, participants were trained to memorize learned (i.e., repeated) colors, which ultimately became stored in LTM; while in the retrieval task, participants had to retrieve the colors from LTM. As indicated above, WM is a memory system with limited capacity (Cowan, 2001) and recent neuroscience studies have shown that encoding information into WM can be measured by frequency-specific oscillations in EEG signals (Erickson et al., 2017; Foster et al., 2016; Fukuda et al., 2016). Specially, the magnitude of suppression in alpha-band oscillations (8-13 Hz) measured across parieto-occipital regions reaches a plateau when the maximum WM storage capacity is occupied. In Fukuda and Woodman (2017) when comparing old information retrieved from LTM and new information encoded into WM, the results showed that the number of colors that could be retrieved from LTM was limited to the maximum WM storage capacity. Also, the magnitude of suppression in alpha-band oscillations that tracked WM storage capacity also tracked the storage of information retrieved from LTM, implicating that WM buffers LTM retrieval.

Fukuda and Woodman's (2017) findings indicate that WM capacity is the limiting factor in the amount of information that can be retrieved from LTM. Note, however, that in their study, WM was not taxed when participants had to retrieve information from LTM. Therefore, it is quite feasible that if WM is not engaged yet, it is adopted to accommodate information retrieved from LTM; Yet, it is unclear what would happen when WM is fully engaged. That is, when no storage space is left in WM, can people still retrieve information from LTM? If so, if WM cannot be used to retrieve information from LTM what other mechanism can be used? In the current study we wanted to determine the neural represen-

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tation of retrieving information from LTM when WM capacity is fully engaged.

To explore these questions, in the current study, we employed a task in which participants had to keep information (i.e., two or four colors) active in WM while *simultaneously* had to retrieve information (i.e., two colors) from LTM (namely, the LTM plus WM condition). The number of colors for WM was determined based on the classic viewpoint that WM capacity is limited to 3-4 items (Cowan, 2001). Therefore, we assumed that when memorizing 4 colors into WM, it is fully engaged. The extent to which WM is fully engaged is further examined by our behavioral and neural findings. We compared the LTM retrieval plus WM condition to a condition in which participants *only* had to keep two or four colors into WM (namely, the WM condition), and collected behavioral (Exp. 1 and 2) and EEG (Exp. 3) data.

Experiment 1

Participants were trained to memorize four different color arrays into LTM, each having two distinct colors. After learning these colors, participants performed another task in which they stored two or four colors from new color arrays into WM only (i.e., the WM condition), or they stored two or four colors into WM and simultaneously were asked to retrieve two colors from LTM (i.e., the LTM plus WM condition). We reasoned that if participants memorized four new colors into WM, its capacity would reach its maximum (Cowan, 2001). So, if retrieving information from LTM is still possible when WM is fully engaged, the overall memory performance in the LTM plus WM condition would be better than that observed in the WM condition. If not, we expect that memory storage in the LTM plus WM condition would be limited to the maximum WM capacity observed in the WM condition.

Method

Participants

Sixteen college students (1 man and 15 women with a mean age of 19.8 years old) were recruited from Zhejiang Normal University and participated for monetary compensation. Sample size was predetermined based on the main effect of memory condition (*WM* vs. *LTM plus WM*) in the pilot study (N= 4), *partial* η^2 = .99. With 16 subjects and alpha = .001, power for the critical effect should be larger than .99. All participants reported normal color vision, and normal or corrected-to-normal visual acuity. Written consent was obtained from all of them, and the study was approved by the Scientific and Ethics Review Committee of the Faculty of Behavioral and Movement Sciences of the Vrije Universiteit Amsterdam (VCWE-2016-215) and the ethical committee of Zhejiang Normal University (ZJNU-2020006).

Apparatus and stimuli

Participants were tested in a dimly lit laboratory and were required to rest their chin on the chin rest 70 cm away from an LCD (Liquid Crystal Display) monitor, 1600 × 900 resolutions with 60 Hz refresh rate, on which visual stimuli were presented against a gray (red-green-blue: 128, 128, 128) background. Stimulus presentation and response registration were controlled by scripts written in Python. The color squares (subtended by 1.3° × 1.3°) carried different to-be-memorized colors, which were randomly chosen from the equal-luminance color set (red-green-blue: Royal Blue [58, 105, 230], Amethyst [134, 85, 206], Deep Cerise [217, 68, 135], Radical Red [243, 66, 76], Fiery Orange [185, 87, 34], Pesto [119, 107, 33], Bilbao [64, 122, 53], Dark Cyan [10, 129, 139]).

Procedure and design

During LTM training, as illustrated in Fig. 1A, a central white dot (illustrated in black in the figure) with a radius of 0.2° and six 3 × 3 grids, each subtending 4.3° × 4.3° centered 6° eccentric to the screen center, were presented throughout the trial. Seven hundred milliseconds after a trial started, an array of two to-be-memorized color squares always appeared at fixed locations in the two top grids for 150 ms respectively, followed by an 850 ms interval. Within each grid, the col (Fernandes and Moscovitch, 2000)or squares could appear at any location. At the end of the trial, a black square indicating the to-be-recalled item was presented in one of previous color squares' locations until the response was collected. Participants were required to report the probe color by pressing a corresponding key on the keyboard (from 8 potential keys mapped to the eight possible colors). If participants made an error, auditory feedback was given after the trial. The inter-trial interval was randomly chosen from 200 – 400 ms. Participants finished 25 blocks of 48 trials (including 16 new trials and 32 to-be-learned trials). Note that, similar to Fukuda and Woodman (2017), we offer enough training to ensure that information was indeed stored in LTM, rather than presenting items sequentially for a short period (Fernandes and Moscovitch, 2000). In the probe display, a letter cue (A, B, C, or D for learned arrays and N for new arrays) was presented at the center of the screen so that participants could learn the associations between the letter cue and the color array. Each letter cue was associated with two colors that each appeared at a fixed location within a unique grid at the top (e.g., red in location X in the top left grid and green in location Y in the top right grid were associated with one specific letter cue). Participants had to memorize both the colors and their corresponding locations. Importantly, to ensure the cue was informative, each letter cue could be associated with the identical location but with different colors (e.g., red in location X in the top left grid for the letter cue A on one trial, and yellow in the same location and the same grid for the letter cue B on another trial).

After LTM training, participants were asked to perform a main memory task. The procedure for the main task was illustrated in Fig. 1B. In the WM condition, 1200 ms after the trial started, a new color array consisting of two or four color squares appeared in two or four grids for 500 ms respectively (which never appeared in the two top grids for the

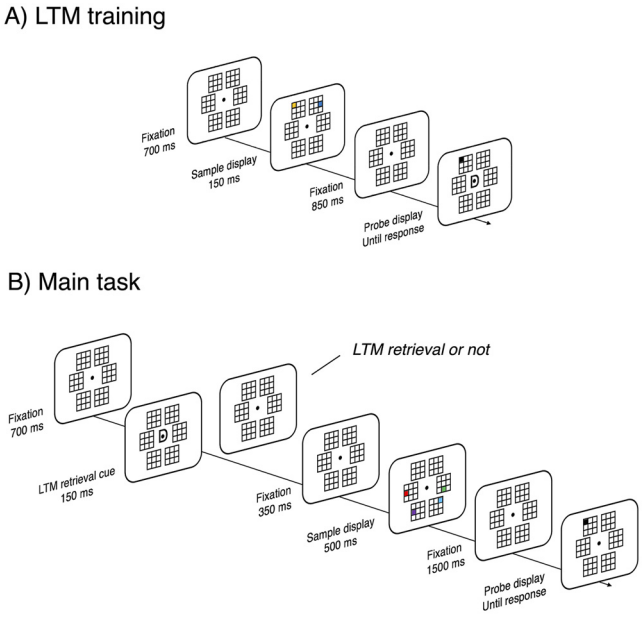


Fig. 1. The experimental procedure in Experiment 1. A) LTM training, in which participants are trained to memorize different arrays of two colors into LTM by associating each array with a unique letter cue presented during the probe period. B) Main task, in which participants have to memorize two or four colors from new color arrays into WM only (i.e., WM condition), or have to memorize two or four colors into WM and simultaneously retrieve two colors from LTM (i.e., LTM plus WM condition). The subsequent test could be on items for either WM or LTM.

learned arrays from LTM training, and the location was randomly chosen from four bottom grids when the new array size was two), followed by a 1500 ms interval. Then, a probe display appeared with a black square indicating the location of the to-be-recalled color (belonged to new color array) until the response was collected.

While in the LTM plus WM condition, a learned letter cue appeared 350 ms before the new color array for 150 ms, instructing participants to start retrieving the corresponding color array from LTM immediately. Note that, by means of EEG, Fukuda and Woodman (2017) showed that the whole color array was retrieved immediately when the cue was presented, as alpha power (i.e., an index for memory storage) increased with array size increase around 800 ms after the cue onset. After a 1500 ms interval, a probe display appeared with a black square located at the location of the to-be-recalled color (belonged to either new or learned color array) until the response was collected. Within each grid, the color squares could appear at any location. Each item in different memory conditions (WM and LTM plus WM) had equal chance to be tested. If participants committed an error, auditory feedback was given after the trial. The inter-trial interval was randomly chosen from 200 – 400 ms.

Both conditions were randomly mixed within blocks, while different set sizes of the new color array (two and four) were tested in different blocks and the testing order was counterbalanced between subjects. Thus, a 2 (new array size: *two* vs. *four*) × 2 (memory condition: *WM* vs. *LTM plus WM*) within-subjects design was adopted. Participants finished 12 blocks of 60 trials (i.e., 180 trials for each new array size and each memory condition).

Analysis

To evaluate the overall memory performance, we adopted the same method as presented in Fukuda and Woodman (2017). Thus, the accuracy was converted to memory capacity (K), an estimate of the number of memorized objects. Eight possible answers could be chosen for each response, participants had a chance to correctly guess response with the probability of 1/8. When participants were required to memorize an array of objects (with the array size of S), the accuracy (A) could be the sum of K/S (for correct response trials) and $(S\text{-}K)/S\times 1/8$ (for guessing trials). By converting this equation, the memory capacity was calculated with the equation: $K = 8/7\times S\times(A–1/8)$. In the WM condition, the memory capacity of items that can be maintained is directly converted from accuracy with former equation. In the LTM plus WM condition, the calculated memory capacity is the sum of the memory capacity for new arrays and the memory capacity for learned arrays.

Results

LTM training

The mean accuracy for the new and learned arrays is presented in Fig. 2A left panel. For the learned arrays, a repeated measures ANOVA with block as a factor revealed a significant main effect, $F(24, 360) = 16.68$, $p < .001$, partial $\eta^2 = .53$. Clearly, due to training, memory performance was improved, with a final accuracy of 0.95 ± 0.01, which was significantly higher than the average accuracy of the new arrays (0.85 ± 0.02), $t(15) = 4.15$, $p < .001$, $d = 1.37$. It suggests that participants have learned these arrays and stored them into LTM.

Main task

The accuracy was converted to memory capacity (K), an estimate of the number of memorized objects (see Fukuda and Woodman, 2017 for similar manipulation). The mean capacity for each condition and each new array size is presented in Fig. 2B left panel. A 2 (new array size: *two* vs. *four*) × 2 (memory condition: *LTM plus WM* vs. *WM*) repeated measures ANOVA on mean capacity showed significant main effects for new array size, $F(1, 15) = 40.55$, $p < .001$, partial $\eta^2 = .73$, and memory condition, $F(1,15) = 411.64$, $p < .001$, partial $\eta^2 = .97$. The memory performance was better when the new array size was four (3.35 ± 0.17) compared to when it was two (2.66 ± 0.07). Importantly, participants recalled more items in the LTM plus WM condition (3.87 + 0.59) than in the WM condition (2.14 ± 0.09). The interaction was far from reliable, $F(1, 15) < 0.01$, $p = .99$, partial $\eta^2 < .01$. The current results indicate that, when WM is fully engaged (i.e., new array size four), retrieving information from LTM is still possible. The maximum number of stored items in the LTM plus WM condition is not limited to the maximum WM capacity.

Another interesting finding is that, compared to memorizing two colors into WM, the calculated capacity was increased ~0.7 items when memorizing four colors into WM; while it was increased ~1.7 items when retrieving two colors from LTM and simultaneously memorizing two colors into WM. Although the total number of to-be-stored items was four in both conditions, participants stored more items in the LTM plus WM condition relative to the WM condition, $t(15) = 9.35$, $p < .001$ (FDR corrected), $d = 2.34$. It indicates that retrieving information from LTM is different from encoding information into WM; otherwise, the increased capacity should be the same as the total number of to-be-stored items is fixed at four.

Experiment 2

In Experiment 1, once the probe display with black squares appeared, participants knew whether they would be tested on items from LTM (located in the two top grids) or on items from WM (located in the four bottom grids). They knew this because a probe was positioned in the two top grids indicating the retrieval from LTM and a probe was positioned in the four bottom grids implying the retrieval from WM. Therefore, this information could be used to strategically forget one type of memory (i.e., LTM or WM) before a response was given. To eliminate this concern in Experiment 2 we always had two probe displays testing both types of memory representations in the LTM plus WM condition (see Fig. 3).

Method

Sixteen college students (2 men and 14 women with a mean age of 19.2 years old) were recruited. The procedure was the same as in Experiment 1, except that after the learned color arrays from LTM were tested, the colors from new arrays were tested as well in the LTM plus WM condition (Fig. 3). Note that only the learned color arrays from LTM were tested in the first probe display. The second probe display (for testing new items) appeared 500 ms after the first probe display (for testing learned items from LTM); while in the WM condition, a 2000 ms interval was introduced to match the time before the second probe display between different conditions. For each probe display, participants were required to report the probe color by pressing a corresponding key on the keyboard immediately when the probe display was presented.

Results

LTM training

The mean accuracy for the new and learned arrays is presented in Fig. 2A middle panel. For the learned arrays, a repeated measures ANOVA with block as a factor revealed a significant main effect, $F(24, 360) = 16.68$, $p < .001$, partial $\eta^2 = .53$. Again, the memory performance was improved after training, with the final accuracy of 0.97 ± 0.01, which was significantly higher than the average accuracy of the new arrays (0.83 ± 0.02), $t(15) = 6.78$, $p < .001$, $d = 2.27$.

Main task

The mean capacity for each condition and each new array size is presented in Fig. 2B middle panel. A 2 (new array size: *two* vs. *four*)

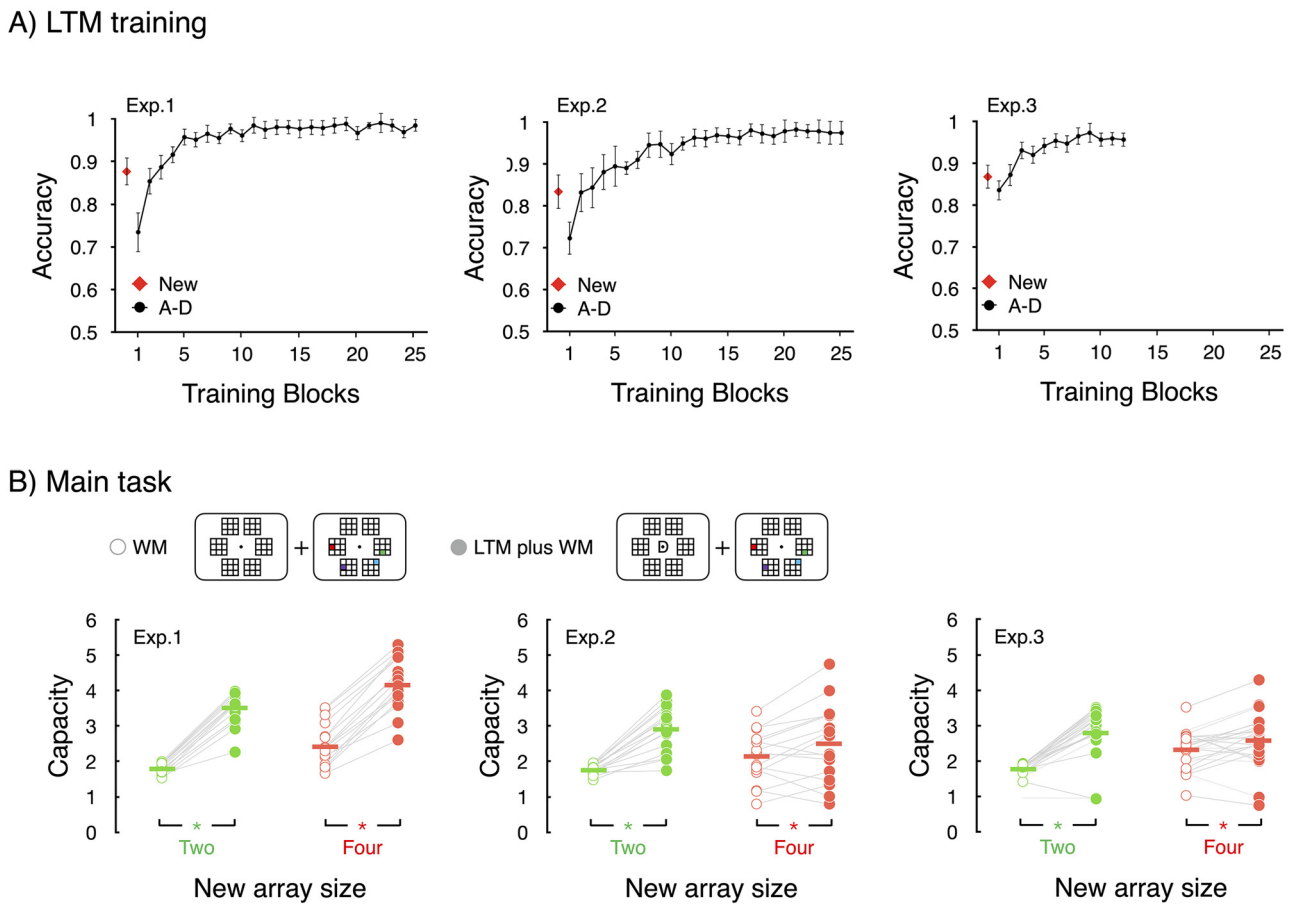


Fig. 2. A) The results for the LTM training in Experiment 1 (left panel), 2 (middle panel), and 3 (right panel), it shows that after training participants' memory performance for learned color arrays reaches a plateau, suggesting that those colors are stored in LTM. B) The calculated capacity for different new array sizes and different memory conditions for the main task in Experiment 1 (left panel), 2 (middle panel), and 3 (left panel). Error bars represent 95% CIs.

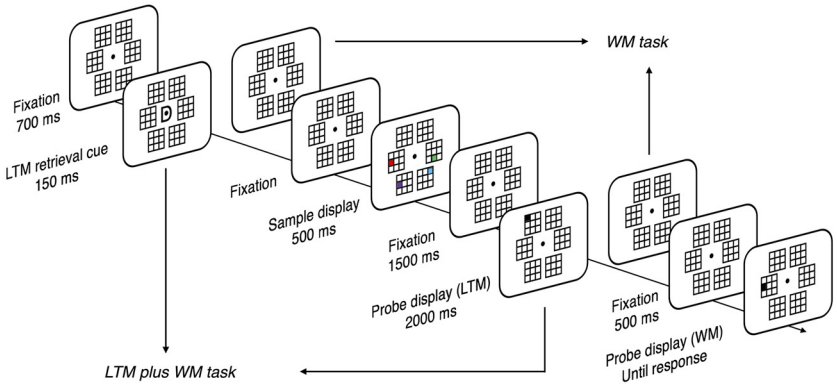


Fig. 3. The experimental procedure for the main task in Experiments 2 and 3. Participants memorize two or four colors from new color arrays into WM only (i.e., WM condition), or memorize two or four colors from new color arrays into WM and simultaneously are asked to retrieve two colors from LTM (i.e., LTM plus WM condition). The test is conducted on LTM and WM sequentially in the LTM plus WM condition.

× 2 (memory condition: *LTM plus WM* vs. *WM*) repeated measures ANOVA on mean capacity showed a main effect for memory condition, $F(1,15) = 31.52$, $p < .001$, partial $\eta^2 = .68$, but not for new array size, $F(1, 15) = 0.03$, $p = .86$, partial $\eta^2 < .01$. Again, critically, participants could recall more items in the LTM plus WM condition (2.7 ± 0.2) than in the WM condition (1.96 ± 0.1). A significant two-way interaction was observed, $F(1, 15) = 32.49$, $p < .001$, partial $\eta^2 = .68$. Planned comparisons confirmed the critical findings of Experiment 1, showing that the overall memory performance was significantly better in the LTM plus WM condition when the new array size was two, $p < .001$ (FDR corrected), and such improvement was marginally significant when the new array size was four, $p = .037$ (uncorrected; FDR corrected $p = .056$), suggesting that information can be successfully retrieved from LTM when WM is fully engaged.

Again, compared to memorizing two colors into WM, the calculated capacity was increased ~0.3 items when memorizing four colors into WM; while it was increased ~1.1 items when retrieving two colors from LTM and simultaneously memorizing two colors into WM. Although the total number of to-be-stored items was four in both conditions, participants stored more items in the LTM plus WM condition relative to the WM condition, $t(15) = 4.84$, $p < .001$ (FDR corrected), $d = 1.21$, indicating that retrieving information from LTM is different from encoding information into WM.

The results in Experiments 1 and 2 consistently indicated that, when encoding 4 items into WM, additional items can still be retrieved from LTM successfully by showing that calculated memory capacity increased with ~1.2 more items. Here we observed an interaction between new array size and memory condition in Experiment 2, which is quite possi-

ble due to the dual-task interference which impacts WM representations stronger when the new array size was four than when the new array size was two. This is consistent with previous findings which showed that WM representations are affected when a secondary task needs to be performed during the retention interval (Nieuwenstein and Wyble, 2014; B. Wang et al., 2018).

Experiment 3

Even though traditionally it has been assumed that information retrieved from LTM has to be represented in WM, only recently there has been neurophysiological evidence confirming this notion (Fukuda and Woodman, 2017). It was shown that retrieving information from LTM was also limited to a few of objects, eliciting a pattern of neurophysiological activity (i.e., the suppression of power in alpha-band in EEG signals) that was similar to storing new information into WM (Fukuda and Woodman, 2017). However, based on our behavioral findings of Experiments 1 and 2, we assume that there might exist another cognitive mechanism supporting LTM retrieval, which might elicit a pattern of neurophysiological activity that is similar as storing new information into WM. In Experiment 3, we replicated Experiment 2 while recording EEG (see Fig. 3 for the task).

Similar to Fukuda and Woodman, 2017, the suppression within the alpha band is used as the neural marker to track LTM retrieval. Originally, the magnitude of the global alpha suppression is assumed to track WM capacity (Adam et al., 2018; Fukuda et al., 2015, 2016; Fukuda and Woodman, 2017) reflecting WM representations. However, a recent study indicated that the global alpha suppression may not reflect WM storage, but instead reflect *an attentional* mechanism (Wang et al., 2021). In Wang et al. (2021), participants were asked to memorize one item with different numbers of distractors, and the results showed that the magnitude of the global alpha suppression was boosted when the number of distractors increased. Although this may imply that global alpha suppression simply reflects the total amount of visual input, Wang et al. (2021) ruled out this possibility by showing that global alpha suppression has its limit and no longer increases even when the total amount of sensory input continues to increase. Similarly, Fukuda and Woodman (2017) showed that global alpha suppression no longer increases when it reaches maximum WM capacity (Fukuda et al., 2015, 2016). Thus, two conservative implications regarding global alpha suppression can be drawn. That is,

I1: *Global alpha suppression reflects a non-specific attentional mechanism (which is involved in WM task and LTM retrieval), and its magnitude is related to the attentional load required for the task.*

I2: *Critically, it has its magnitude limit and stops increasing when the total information exceeds the maximum information that can be processed within the same task (e.g., maximum amount of visual input in visual processing, or maximum WM capacity in WM task).*

Furthermore, empirical studies exploring lateralized alpha suppression suggest that any change in alpha oscillation is related to multiple cognitive aspects, such as task difficulty, cognitive load, or attentional selection (e.g., Günseli et al. 2019; Hakim et al. 2019; Vries, Driel, and Olivers 2017; Wang et al. 2019). However, it should be noted that these findings convergingly showed that lower alpha power reflects more attentional resources needed for the employed task set. In this sense, extra global alpha suppression implies that more attentional resources are needed according to the task requirements. Thus, we speculate that:

I3: *Once the magnitude of global alpha suppression reached its plateau in a WM task, any extra alpha suppression observed cannot be due to any further WM processing (based on implication 2). So, such extra suppression may reflect another cognitive process related to the task requirement (e.g., LTM retrieval is assumed in the present study), which consumes more attentional resources.*

Based on these three implications, we first examined whether WM capacity reached its plateau in the WM condition by comparing the magnitude of the global alpha suppression between new array sizes two and four. If the magnitude is the same between different new array sizes in the WM condition, it suggests that WM capacity reached its plateau for both new array sizes. Furthermore, we continued to examine whether the maximum suppression in alpha oscillation can be further suppressed in the LTM plus WM condition. If so, it indicates that extra attentional resources are needed for the new cognitive process when keeping maximum number of items in WM. It should be noted that this cannot be contributed to by further WM processing (refer to above implications 2 and 3); instead it suggests that LTM retrieval should be considered as a different (novel) cognitive process when WM is fully engaged, as it does not always require the involvement of WM. In all other situations, WM is the core mechanism for LTM retrieval.

Method

Twenty-four college students (8 men and 16 women with a mean age of 20.5 years old). The procedure was identical to that in Experiment 2, except that the number of training blocks was reduced to 12 as we estimated that this should be enough training to store items into LTM. Moreover, Fukuda and Woodman (2017) showed that alpha-band oscillation tracking WM content starts about ~200 ms after the memory array onset, while that tracking LTM content starts ~800 ms after the retrieval cue onset. Therefore, we increased the interval between cue display and sample display from 350 ms to 450 ms to match the latency of alpha-band oscillation between WM and LTM tasks, allowing us to simultaneously investigate the neuro-traces underlying LTM retrieval and WM.

EEG data recording and preprocessing

With the sample rate of 512 Hz, EEG data were recorded from 64 electrodes through a BioSemi ActiveTwo system, that were placed according to international 10–20 system. To monitor eye movements, the vertical electro-oculogram (EOG) was recorded from electrodes located 2 cm above and below the right eye, and the horizontal EOG was recorded from electrodes 1 cm lateral to the external canthi.

EEG data were re-referenced to the mean of the left and right earlobes and were high-pass filtered using a cut-off of 1.5 Hz (for independent component analysis [ICA] only) and 0.1 Hz (for final analysis). High-pass filtering was done with default setting of the pop_basicfilter function of ERPLAB (Lopez-Calderon and Luck, 2014), using a Butterworth IIR filter. Continuous EEG was epoched from -2.0 to 6 s relative to the onset of the cue display (to avoid edge artifacts resulting from wavelet convolution). Trial rejection and ICA were done on smaller epochs (-1.0 to 5 s) to avoid overlapping time points across epochs. Epochs were baseline-normalized by using the whole epoch as baseline to improve ICA (Groppe et al., 2009).

Malfunctioning electrodes were visually detected and temporarily removed from the data (average 1.83 electrodes per subjects were removed and replaced later). Electromygram (EMG) artifacts were detected and rejected by using an adapted version of an automatic trial-rejection procedure as implemented in the Fieldtrip toolbox (Oostenveld et al., 2011). Here we used a 110-140 Hz bandpass filter to capture high-frequency muscle activity, and allowed for variable z-score cutoffs per subject based on the within-subject variance of z-scores. After trial rejection, ICA as implemented in the EEGLAB toolbox (Delorme and Makeig, 2004) was performed on the clean electrodes only. Combining with the EOG signals, we visually inspected and removed ICA components that captured eye blinks, eye-movement, or other artifacts that were not brain-driven activity. Afterwards, the malfunctioning electrodes identified earlier were interpolated through spherical spline interpolation as implemented in eeg_interp.m function in EEGLAB. All steps together left 86 ± 1.5% trials (~155 trials per condition) for further analysis.

Time-frequency analysis

We decomposed the epoched EEG time series into time-frequency representations with custom-written MATLAB scripts (github.com/joramvd/tfdecomp). The time series were convolved with a set of Morlet wavelets with frequencies ranging from 1 to 40 Hz in 25 logarithmically spaced steps. The complex wavelets were created by multiplying perfect sine waves ($e^{i2\pi ft}$, where i is the complex operator, f is frequency, and t is time) with a Gaussian ($e^{-t^2/2s^2}$, where s is the width of the Gaussian). The width of the Gaussian was set as $s = \delta/(2\pi f)$, where δ represents the number of cycles of each wavelet, logarithmically spaced between 3 (for 1 Hz) and 12 (for 40 Hz) to have a good trade-off between temporal and frequency precision. In the frequency domain convolution was applied: The Fast Fourier Transform was applied to both the EEG data and the Morlet wavelets, and these were multiplied. The results were then converted back to the time domain through the inverse fast Fourier transform. The frequency-specific power at each time point was calculated as the squared magnitude of the complex signal from the convolution [real$(Z_t)^2$ + imag$(Z_t)^2$].

Raw power was averaged over trials per condition, after which it was decibel normalized [dB Power_{tf} = 10*log10(Power_{tf} / Baseline Power_f)] for each frequency and channel, with the baseline defined as the condition-average power in the period of 500 to 200 ms before the cue display onset. Since we specifically were interested in the parieto-occipital alpha-band oscillation, and thus the calculated power between 8-13 Hz at parieto-occipital electrodes (P3/4, PO3/4, O1/2, and Pz) were averaged across time points (referred to Fukuda and Woodman, 2017).

Statistics of EEG data

Since we had no hypothesis that at which time point there would be a difference in alpha-band oscillation between the WM and LTM plus WM conditions, we started an exploring analysis with the classic permutation-based approach with cluster-size correction. Specifically, we used paired t-tests to compare different conditions on alpha power over time; at each test, the sign of the power values was shuffled across subjects in 2000 permutations to yield a null-distribution against which observed clusters of summed t-values were thresholded using $p < 0.05$.

Results

LTM training

The mean accuracy for the new and learned arrays is presented in Fig. 2A right panel. For the learned arrays, a repeated measures ANOVA with block as a factor revealed a significant main effect, $F(11, 264) = 14.8$, $p < .001$, partial $\eta^2 = .39$. The memory performance was improved after training, with the final accuracy of 0.95 ± 0.01, which was significantly higher than the average accuracy of the new arrays (0.87 ± 0.01), $t(23) = 6.92$, $p < .001$, $d = 1.41$.

Main task

The mean capacity for each condition and each new array size is presented in Fig. 2B right panel. A 2 (new array size: *two* vs. *four*) × 2 (memory condition: *LTM plus WM* vs. *WM*) repeated measures ANOVA on mean capacity showed a main effect for memory condition, $F(1,23) = 50.5$, $p < .001$, partial $\eta^2 = .69$, but not for new array size, $F(1, 23) = 2.11$, $p = .16$, partial $\eta^2 = .08$. Participants could recall more items in the LTM plus WM condition (2.73 ± 0.1) than in the WM (2.04 ± 0.07), $t(23) = 7.11$, $p < .001$, $d = 1.45$. A significant two-way interaction was observed, $F(1, 23) = 91.31$, $p < .001$, partial $\eta^2 = .8$. Consistent with Experiments 1 and 2, we again found that the overall memory performance was significantly better in the LTM plus WM condition when the new array size was two, $p < .001$ (FDR corrected). Although the improvement was marginally significant when the new array size was four in Exp. 2, here we observed significant improvement with larger sample size, $p = .028$ (FDR corrected).

Again, compared to memorizing two colors into WM, the calculated capacity was increased ~0.6 items when memorizing four colors into WM; while it was increased ~1.1 items when retrieving two colors from LTM and simultaneously memorizing two colors into WM. The difference between conditions reached significance, $t(15) = 4.84$, $p = .002$ (FDR corrected), $d = 1.21$, indicating that retrieving information from LTM is different from encoding information into WM.

Parieto-occipital alpha oscillation

To further explore the neural mechanism behind LTM retrieval and its interaction with WM, we investigated alpha oscillation (8-13 Hz) at parieto-occipital electrodes and observed a strong global alpha suppression in both the WM and LTM plus WM condition (see Fig. 4).

In all three experiments, the behavioral findings of the WM condition showed that participants can only memorize ~2 items into WM in the present study. When comparing the new array size two and four in the WM condition, the cluster-based permutation test on the alpha-band revealed no reliable difference over the whole time series (see Fig. 4A), confirming that there is no extra capacity available in WM for both new array sizes as global alpha suppression plateaus at this level (according to our previous interpretations 2 and 3). This is consistent with previous studies (Fukuda et al., 2015; Fukuda and Woodman, 2017; Sauseng et al., 2009), showing that once WM reaches its maximum capacity, the magnitude of global alpha suppression tracking this behavioral finding also reaches its maximum. This in turn reflects that any further increase in alpha suppression cannot be attribute to the operation of WM (refer to previous interpretation 3).

Thus, based on this assumption, we compared the LTM plus WM condition and WM condition. The cluster-based permutation test showed that there was stronger suppression in the alpha-band in the LTM plus WM condition than the WM condition regardless of the number of items stored in WM. As shown in Fig. 4B, when the new array size was two, there was steeper suppression for the LTM plus WM condition than the WM condition, from ~300 ms to ~2700 ms, and from ~3100 ms to ~4700 ms following the presentation of the LTM retrieval cue, which was confirmed by paired t-tests between the averaged alpha power in those time windows, both ts > 4.1, ps < .001. That is, as soon as the LTM retrieval cue is presented, there is a sharp drop in alpha suppression. We argue that this sharp drop in alpha suppression represents the neural response of LTM retrieval when WM is fully engaged (see Fig. 4B bottom panel).

Note that, the significant time windows reported above covered the encoding and storage periods of WM. It implies that LTM retrieval operates independent of the encoding and storage in WM. The initial drop in alpha suppression following the presentation of the LTM retrieval cue provides extra store space in addition to the stored WM contents. When the first probe display was presented information from LTM needed to be reactivated, as a result we observed a strong drop in alpha suppression again. It indicates that LTM retrieval was activated again to finish the task. If by this time, information that originally was retrieved from LTM now would have been available in WM we would not have expected to see such a sharp drop again. This also implies that LTM retrieval might be triggered by both the retrieval cue and the LTM probe. We will return to this discussion later.

For new array size four, as illustrated in Fig. 4C, we observed basically the same pattern: there was steeper alpha suppression for the LTM plus WM condition than that for the WM condition, from ~300 ms to ~1400 ms, and from ~3100 ms to ~3900 ms after the presentation of the LTM retrieval cue, which was confirmed by paired t-tests between the averaged alpha power in those time windows, both ts > 3, ps < .007.

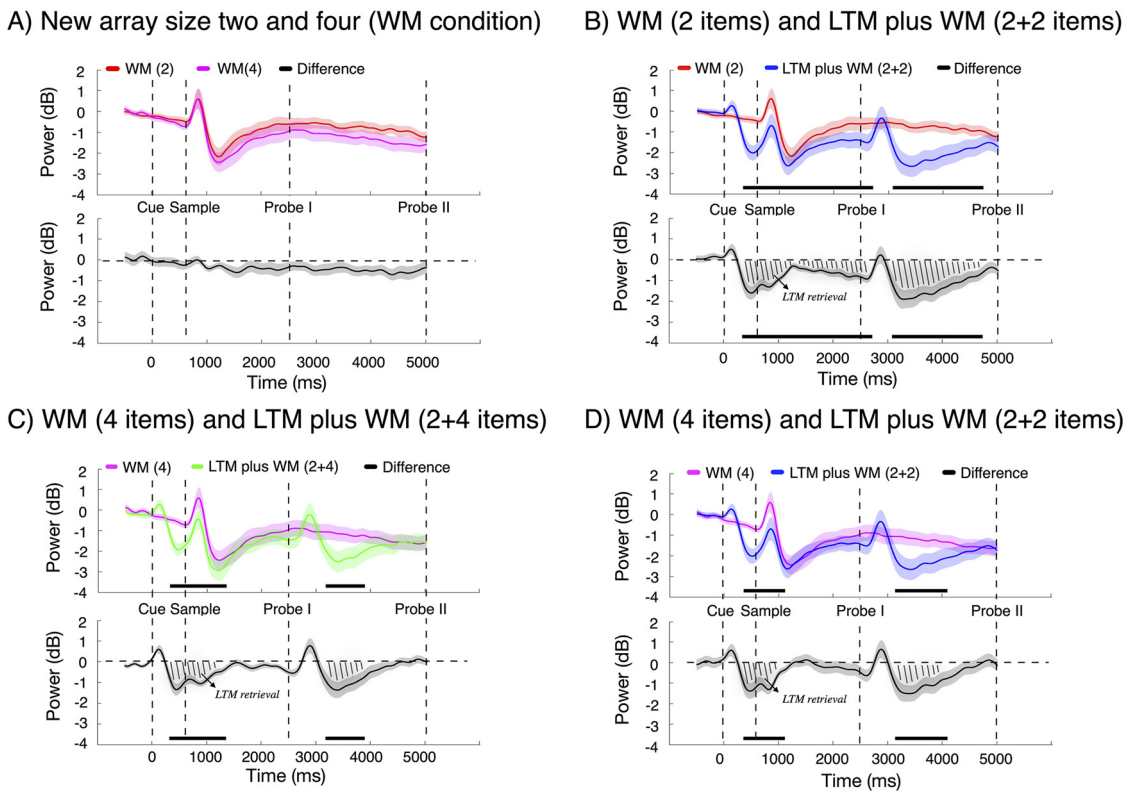


Fig. 4. The comparison between the suppression in alpha-band in different conditions in Experiment 3. The comparisons are conducted between different new array sizes in the WM condition (A), between the WM and LTM plus WM conditions for new array size two (B) and four (C), and between the WM (new array size four) and LTM plus WM (new array size two) conditions when the total number of memory items was kept constant at four. The electrodes, PO3/4, P3/4, O1/2, Pz, are selected for analysis. Black horizontal bars indicate significant clusters (at $\alpha = 0.05$) as produced by cluster-based permutation testing. The error bars show the within-subject SEM.

Finally, we conducted a further analysis to exclude potential confounds regarding compressing (Brady et al., 2009; Schurgin and Brady, 2019) and/or overwriting. That is, one might speculate that, instead of our claim of independent LTM retrieval, the observed steeper alpha suppression was due to the fact that information retrieved from LTM overwrote WM contents, or that WM content was compressed such that more information could be retrieved into WM. To exclude these alternative explanations, in the new comparisons, we kept the total number of memory items constant at four, and compared the WM condition (when the new array size was four) with the LTM plus WM condition (when the new array size was two). If LTM retrieval overwrites WM contents, we would observe no difference between conditions; and if WM content was compressed when LTM retrieval was involved, we would observe smaller alpha suppression in the LTM plus WM condition. However, we did not observe any effects consistent with these speculations. Instead, as illustrated in Fig. 4D, there was steeper alpha suppression in the LTM plus WM condition again, from ~300 ms to ~1100 ms, and from ~3100 ms to ~4100 ms after the presentation of the LTM retrieval cue. Therefore, it is highly unlikely that WM compression and/or overwriting took place in the current experiments.

One may argue that immediately following initial LTM retrieval, information could still overwrite WM contents. Although this may seem feasible, it is not likely. If the overwriting occurred immediately after LTM retrieval, information retrieved from LTM should already be stored in WM before the first probe display. Then, there is no need to re-activate or re-retrieve information from LTM again. It should be noted that we observed a second drop in global alpha suppression during the first probe period when comparing the LTM plus WM condition with the WM condition. By this time, information that originally was retrieved from LTM was no longer available in WM, making overwriting unlikely. Another possibility regarding overwriting account is that while LTM retrieval can bypass WM, LTM retrieval may still partially overwrite the WM contents. To address this concern, we conducted an analysis in which we estimated capacity for WM and LTM retrieval separately in the LTM plus WM condition. If WM and LTM retrieval share memory resources, then a negative correlation between them should be found. However, the results showed that there was no negative correlation between WM capacity and LTM retrieval capacity for new array size two and four in Experiments 2 and 3; instead we observed positive correlations for new array size two in both experiments, both $rs > 0.49$, $ps < .014$. It suggests that there was no trade-off between LTM retrieval and WM storage, i.e., there is no evidence for partially overwriting.

Overall, the current findings indicate that LTM retrieval does not necessarily rely on the involvement of WM, when WM is fully engaged. We observed that when more than 2 items needed to be encoded and stored into WM (Fig. 4A), the magnitude of alpha suppression was at its maximum. Yet, when more items needed to be retrieved from LTM (Fig. 4B and 4C), alpha suppression was even stronger, expanding its capacity above and beyond the maximum capacity of WM. Combining with the evidence regarding alpha suppression we summarized before, we argue that the increase in memory capacity in the LTM plus WM condition operates outside WM, possibly reflecting another way dedicated for LTM retrieval.

General discussion

For decades, it was assumed that when humans retrieve information from LTM, they do this by bringing this information back into WM so that they can employ this information for ongoing tasks (Atkinson and Shiffrin, 1968; Broadbent, 1975; James, 1890). However, as it is well known that WM capacity is limited (e.g., Cowan, 2001), it was unclear what would happen for LTM retrieval when WM would be fully engaged.

In all three experiments, the behavioral results showed that no matter how many new colors were required to be maintained in WM, the overall memory performance in the LTM plus WM condition was better compared to that in the WM condition, suggesting that retrieving information from LTM is possible even when WM capacity is fully occupied. In Experiment 3 using EEG recording, it was shown that the suppression in alpha-band reached a plateau representing the maximum WM capacity. However, when information needed to be retrieved from LTM, alpha suppression was even further increased. Based on our previous interpretations regarding alpha suppression, the extra alpha suppression observed cannot be due to storing information in WM, as WM is fully occupied. The only reason is the involvement of LTM (the sharp drop in alpha suppression following the LTM cue), which rides on top of the alpha pattern that is generated by the involvement of WM (the pattern following the sample display). This provides direct evidence that the encoding and storage in WM operates independent of the LTM retrieval.

On the basis of these findings we conclude that information retrieved from LTM does not always have to be brought back into WM, but instead might be accessed differently when WM is fully engaged. Before accepting such a conclusion there are several potential confounds to be considered.

Storing retrieved information into WM or dual-task interference?

As we observed interactions between new array size and memory condition in Experiments 2 and 3, one might question whether this indicates that items retrieved from LTM were stored in WM, resulting in memory deficit. It should be noted that, our results indicated that compared to encoding 2 new items into WM, no extra items could be added when encoding 4 new items into WM, suggesting that the WM system was fully engaged. Especially, when encoding 4 items into WM, additional items could still be retrieved from LTM successfully by showing that calculated memory capacity increased with ~1.2 and ~1.1 more items in Experiments 2 and 3. Clearly, this would be impossible if items retrieved from LTM were stored into WM. Importantly, our neural evidence mimicked those behavioral findings, showing that extra alpha suppression reflecting LTM retrieval tracked the additional retrieved items. Therefore, we argue that the only reason for the observed memory deficit is the dual-task interference which impacts WM representations, and possibly LTM retrieval. As shown in other studies, such dual-task interference is well known (Nieuwenstein and Wyble, 2014; Wang et al., 2018).

Serial encoding or independent LTM retrieval?

As we introduced LTM retrieval and WM encoding sequentially in all experiments, one might question that our results were simply due to serial encoding. However, there are three reasons why this is highly unlikely. First, although serial encoding might possibly enlarge WM capacity, this enlarged capacity still cannot exceed the maximum WM capacity (Mance et al., 2012). We showed that in the WM condition, WM capacity reached its plateau when encoding 4 items. Therefore, it is unlikely that serial encoding can exceed the maximum WM capacity, but LTM retrieval can do so. Second, beyond our speculation, we added a new (supplementary) experiment, in which we asked participants to either serially memorize 2 + 4 items into WM (two-array condition) or only memorize 4 items into WM (one-array condition). If serial encoding can exceed the maximum WM capacity, the memory performance should be superior for the two-array condition than that for one-array condition. However, the results showed that there was no reliable difference between conditions, $t(15) = 1.59$, $p = .13$, $d = 0.24$, BF10 = 0.72 (see Fig. S1). In addition, when comparing the two-array condition with the WM+LTM condition (when new array size was four) in Experiment 1, we observed a clear decline on memory capacity for two-array condition, $t(15) = 4.35$, $p < .001$, $d = 1.21$, suggesting that LTM retrieval plus WM encoding is different from serial encoding items into WM. Finally, previous studies have shown that once the WM capacity reaches its maximum, the amplitude of the neural marker (CDA) representing WM capacity would not be amplified when presenting items sequentially (Berggren and Eimer, 2016). Similarly, it has been shown that alpha suppression is not amplified when presenting items sequentially (Wang et al., 2019; Wang et al., 2021). Based on this evidence and our findings that alpha suppression was further amplified when LTM retrieval was involved, it seems reasonable to argue that LTM retrieval operated outside of fully engaged WM.

Sensory processing or independent LTM retrieval?

Compared to the WM condition, in the LTM plus WM condition participants had to process the retrieval cue first. Therefore, it is feasible that the current findings are due to a difference in sensory processing between conditions. Although sensory input per se could induce suppression in alpha band, it should be noted that the alpha suppression elicited by the sensory input still has a limit, subjected to the maximum amount of sensory input (Wang et al., 2021). As shown in Wang et al. (2021), the magnitude of alpha suppression increased with the number of perceptual distractors, and stopped increasing when the sensory inputs of distractors reached its maximum (i.e., 2 or 3 distractors). If sensory input in our Experiment 3 would have contributed to any of our findings, the magnitude of alpha suppression should have increased when the new array size was four compared to two in the WM condition, as the number of to-be-encoded items increased. However, this is not the case. Instead we found that when comparing the new array size two and four in the WM condition, the cluster-based permutation test on the alpha-band revealed no reliable difference over the whole time series (see Fig. 4A). Therefore, it is unlikely that our results can be explained by extra sensory input in the LTM plus WM condition.

Storing items in WM in a passive state or independent LTM retrieval?

Recent research has shown that items stored in WM can be briefly dropped from an active state into a passive state when doing a second task simultaneously, and then later are brought back online with little or no cost when completing the WM task (LaRocque et al., 2013; Lewis-Peacock et al., 2012; Vries et al., 2017; but see Wang et al., 2018). Even though this explanation seems viable, they do not seem to be consistent with the EEG findings of the current study. Previously it was shown that alpha suppression is smaller for items in a passive state relatively to an active state (Vries et al., 2017). Therefore, if in the current experiment, items would have been stored in a passive state in WM, we would have expected that alpha suppression for WM would be significantly reduced, signified by a relatively shallow alpha suppression in the LTM plus WM condition. Clearly, this was not the case. Instead we observed a stronger alpha suppression in the LTM plus WM condition, suggesting that observers kept the different contents of WM and LTM simultaneously in an active state.

Recent neural evidence suggests shared neural substrates between WM and LTM (Bosch et al., 2014; Favila et al., 2018; Kok Peter et al., 2017). A well-known point is that information retrieved from LTM has to be first brought back into WM for other ongoing tasks (Atkinson and Shiffrin, 1968; Broadbent, 1975; Cantor and Engle, 1993; Nairne and Neath, 2001). Recent studies directly compared WM and LTM representations, investigating how memory systems interact with one another (Fukuda and Woodman, 2017; Öztekin et al., 2010; Vo et al., 2022). They found that both WM and actively retrieved LTMs are supported via the same processes, a capacity-limited state called the “focus of attention” (Cowan, 1995; D’Esposito and Postle, 2015; Fukuda and Woodman, 2017). Moreover, both WM and retrieved LTM contents are represented through the same sensory-like format in the same retinotopic regions in human brain (Vo et al., 2022). Those evidence all point to the claim that LTM retrieval needs WM.

However, it should be noted that the evidence described above was obtained in studies in which WM still had free capacity. This is not always the case, as WM can be fully engaged while doing ongoing cognitive tasks. Our findings that memory performance increased in the LTM plus WM condition relative to the WM condition, indexed by a steeper suppression in alpha oscillation, suggest that LTM retrieval bypasses WM when it is fully engaged. This is not in conflict with any other existing theoretical models, but instead that adds important boundary conditions.

There has been a long debate regarding the role of WM, and how it relates to the encoding and processing of information retrieved from LTM. One prominent theory is that WM and LTM involve separate stores, and that within the WM store there exist different storage modules for different (visual, verbal, and spatial) contents (Baddeley, 2000, 2003; Norris, 2017). Similar to this, Oberauer provides a new theoretical approach, in which it is argued that contents stored in WM are organized through temporary associations (Oberauer, 2009; Oberauer et al., 2013). In contrast to this notion, another prominent theory referred to as the "embedded-processes model" proposed by Cowan (Cowan, 1988, 1999, 2017) suggests that WM is embedded inside LTM. That is, "memory is represented by LTM along with a subset of features that are in a temporarily activated state, making these items more rapidly and reliably accessible than other items in LTM. Within aLTM (activated LTM), a subset of the information is highlighted by the FoA, which includes more processed, integrated information limited to about 3 to 5 independent, coherent units or chunks." (Cowan, 2017). Clearly, the findings of the current study are not decisive regarding these debates but our findings suggest that something like the proposed aLTM might operate for retrieving LTM contents when WM (or FoA) is fully engaged.

It is possible that information is retrieved from LTM into aLTM in an automatic way as soon as the cue that is associated with a memory array is presented (Hebb, 1949). The cue triggers the retrieval of a memory representation from LTM, bypassing the active maintenance of information in WM, reflected by further suppression in alpha oscillation. Information retrieved into LTM could be reactivated again to accomplish the task when the LTM probe was presented, as reflected by a steeper alpha suppression.

Code and data availability

The code we used for preprocessing EEG are available at https://github.com/joramvd/eegpreproc; The code we used for performing time-frequency analysis are available at https://github.com/joramvd/tfdecomp. The behaviour and EEG data can be made available upon reasonable request.

Author notes

JT and BW both act as senior authors. All authors designed the experiment, BL collected and analyzed the data, BL, JT, and BW wrote the paper. All authors approved the final version of the manuscript for submission and declared no competing financial interests. This research was supported by the Key-Area Research and Development Program of Guangdong Province (2019B030335001), the Guangdong Regional Joint Foundation (2019A1515110581), and the National Natural Science Foundation of China (NSFC) grant (32000738) to BW, the European Research Council (ERC) advanced grant 833029 – (LEARNATTEND) to JT. Correspondence should be addressed to Benchi Wang, Institute for Brain Research and Rehabilitation, South China Normal University, Zhongshan Road West 55, Guangzhou, China, 510000. Email: wangbenchi.swift@gmail.com.

Data Availability

Data will be made available on request.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2022.119513.

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