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Cerebral Cortex, 2023, **33**, 10234–10244
https://doi.org/10.1093/cercor/bhad278
Advance access publication date 31 July 2023
Original Article

Neural retrieval processes occur more rapidly for visual mental images that were previously encoded with high-vividness

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Visual mental imagery refers to our ability to experience visual images in the absence of sensory stimulation. Studies have shown that visual mental imagery can improve episodic memory. However, we have limited understanding of the neural mechanisms underlying this improvement. Using electroencephalography, we examined the neural processes associated with the retrieval of previously generated visual mental images, focusing on how the vividness at generation can modulate retrieval processes. Participants viewed word stimuli referring to common objects, forming a visual mental image of each word and rating the vividness of the mental image. This was followed by a surprise old/new recognition task. We compared retrieval performance for items rated as high- versus low-vividness at encoding. High-vividness items were retrieved with faster reaction times and higher confidence ratings in the memory judgment. While controlling for confidence, neural measures indicated that high-vividness items produced an earlier decrease in alpha-band activity at retrieval compared with low-vividness items, suggesting an earlier memory reinstatement. Even when low-vividness items were remembered with high confidence, they were not retrieved as quickly as high-vividness items. These results indicate that when highly vivid mental images are encoded, the speed of their retrieval occurs more rapidly, relative to low-vivid items.

Key words: visual mental imagery; vividness; memory retrieval; EEG; alpha.

Introduction

Imagine that you are studying for a test about DNA replication. You might facilitate your learning by generating a rich visual image of the key structures and processes, which you can then retrieve during the test. Our capacity to experience visual images of events or objects, in the absence of sensory stimulation, is known as "visual imagery" (Pearson 2019). The above example illustrates the fact that individuals can encode visual mental images and retrieve them to aid in performing a memory-dependent task (Maguire et al. 2003; Legge et al. 2012). Although several studies have shown that visual mental imagery can improve memory performance (Gupton and Frincke 1970; Mueller and Jablonski 1970; Bower 1972; McCauley et al. 1996; Foley 2012; D'Angiulli et al. 2013; Gjorgieva et al. 2022), there is relatively little research about the neural mechanisms whereby visual mental images enhance episodic memory.

The scientific study of imagery has explored the neural activations associated with the generation of visual mental images, as well as the modulation of these neural activations according to the ascribed vividness of imagery. Studies have shown that visual imagery generation depends on some of the regions that process visual information itself. Lower-level areas in visual cortex (Kosslyn and Thompson 2003; Lee et al. 2012; but see Spagna et al. 2021), higher-level visual areas (O'Craven and Kanwisher 2000; Pearson et al. 2015), as well as regions in the temporal lobe (Naselaris et al. 2011; Koenig-Robert and Pearson 2019) have all been implicated in the generation of visual imagery. Taken together, these findings support the idea that there is neural overlap between visual perceptual processes and visual imagery processes. However, there are also key differences between visual perception and imagery. The temporal dynamics of visual imagery processes are distinct from visual perceptual processes, evolving later in time (Dijkstra et al. 2018). Additionally, Yu and Postle (2021) found that internally-generated information is represented differently from typical working memory representations of visually perceived items, which are comprised from external sources. Importantly, visual mental imagery has been shown to improve long-term memory performance (Gupton and Frincke 1970; Mueller and Jablonski 1970; Bower 1972; Cornoldi and Paivio 1982; McCauley et al. 1996; Foley 2012; D'Angiulli et al. 2013). These unique functional characteristics of visual mental imagery underscore the necessity of further investigations into the underlying neural processes, and in particular, its role in episodic memory.

One key factor to explore in this regard is vividness, a self-reported expression of the degree of richness and level of detail of a visual mental image (D'Angiulli and Reeves 2007). Vividness has been found to be related to the amount of overlap in neural representation between imagery and perception in the visual and parietal cortices (Dijkstra et al. 2017). Visual mental images can vary greatly in terms of their vividness (Cui et al. 2007), and studies using functional magnetic resonance imaging (fMRI) have shown this variation to modulate neural activation in the precuneus, right parietal cortex, medial frontal cortex, and parts of early visual cortex (Dijkstra et al. 2017). Behaviorally, studies of

Received: February 2, 2023. **Revised:** June 26, 2023. **Accepted:** June 27, 2023
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visual imagery generation have observed faster vividness-rating reaction times (RTs) for more vivid items during the image generation period (D'Angiulli and Reeves 2002; D'Angiulli et al. 2013; Gjorgieva et al. 2022). One hypothesis put forth to explain the RT difference suggests that vividness-rating RTs are representative of the availability of multiple sensory traces in long-term memory (D'Angiulli et al. 2013). Thereby, high-vividness mental images are generated more quickly because sensory traces are more readily available. In addition, studies have shown that more vivid mental images are better remembered (Tulving et al. 1965; Reisberg et al. 1986; De Beni and Pazzaglia 1995; D'Angiulli et al. 2013; Marcotti and St Jacques 2018; Gjorgieva et al. 2022). A previously published paper by our group investigating the encoding of visual mental images found two main differences for those items rated as low-versus high-vividness (Gjorgieva et al. 2022). More specifically, we found that attention was directed internally during the image generation process, and the subsequently remembered low-vividness items were characterized by a longer duration period of internally-directed attention during encoding. In addition, we observed a more sustained event-related potential (ERP) difference due to memory (Dm) at encoding for low-vividness items, suggesting that low-vividness items that were subsequently remembered may have required additional conceptual processing at encoding to compensate for the poor imagery. Taken together, these studies indicate that visual mental imagery can vary in its richness and that this variation has an impact on processing speed and subsequent memory. However, relatively little is known about the neural mechanisms and the time-course by which images with different levels of vividness at encoding are retrieved from episodic memory.

At the electrophysiological level, episodic memory has most commonly been characterized by the parietal old/new effect, an ERP with a positive deflection peaking between 400 and 800 ms over parietal cortex (Curran 2000; Friedman and Johnson 2000; Wilding 2000; Curran 2004; Woodruff et al. 2006; Rugg and Curran 2007). The parietal old/new effect is measured during memory retrieval and has been shown to be modulated by the depth of processing at encoding (Rugg et al. 1998), as well as the amount (Vilberg et al. 2006; Vilberg and Rugg 2009) and quality (Murray et al. 2015; MacLeod and Donaldson 2017) of recollected information at retrieval.

In addition to the parietal ERP, studies have shown that both the amount and the timing of alpha-band EEG desynchronization (i.e. a decrease in the "strength" of the oscillatory activity between 8 and 12 Hz) are associated with the amount of memory retrieved for previously encoded words: improved memory is associated with a bigger and earlier increase in alpha desynchronization (i.e. a decrease in alpha-band power; Martín-Buro et al. 2020). In addition, higher desynchronization in both the alpha (8 and 12 Hz) and low-beta (12 and 20 Hz) frequency bands at retrieval has been associated with higher discrimination between previously encoded images and similar lure images (Karlsson et al. 2020) as well as with the fidelity of the information represented in the cortex (Griffiths et al. 2019). Taken together, these results support the idea that alpha and/or alpha/low-beta desynchronization may reflect the promotion of the information flow to the neural substrates that represent mnemonic content (Klimesch et al. 2007; Hanslmayr et al. 2012; Hanslmayr et al. 2016).

The main objective of the current study was to examine the neural processes associated with the retrieval of previously generated visual mental images, as well as how the vividness of those mental images (self-reported during image generation at encoding) can modulate retrieval processes. To do this, we employed a paradigm composed of two phases while we recorded the EEG activity of human participants (Fig. 1). In the first phase, participants were presented with a series of object-word stimuli (i.e. stimuli that were words referring to objects) and asked to form a mental image of the referent denoted by the word. On each trial, participants then rated the vividness of the mental image they had just formed. In the second phase, participants completed a surprise memory task. During the memory task, participants were presented with both old and new word stimuli and tasked with making a button response to indicate whether the word was old (seen in the first phase) or new (not seen in the first phase) and rate their confidence in that judgment. This experimental paradigm thus allowed us to have a behavioral measure of vividness during encoding, as well as a measure of accuracy and subjective confidence at retrieval (through recognition of the word stimulus cue), while concurrent brain activity data were being recorded. The findings from the encoding phase have been reported in a separate publication (Gjorgieva et al. 2022).

We investigated the retrieval of visual mental images by examining the magnitude of the parietal old/new ERP effect as well as the magnitude and latency of EEG alpha-band power changes. In line with previous research (Rugg and Curran 2007), we expected a modulation of the parietal old/new effect by memory when comparing the activity elicited at retrieval by items subsequently remembered to that elicited by new items that were correctly identified as new. To compare the retrieval of low- vs high-vividness items purely based on vividness, we controlled for memory accuracy and confidence by examining only the items successfully remembered with high confidence. We hypothesized that if high-vividness items were retrieved with increased or improved mnemonic information, we would observe an increased magnitude in the parietal old/new effect (Vilberg et al. 2006; Vilberg and Rugg 2009; Murray et al. 2015). Additionally, we examined the role of alpha-band desynchronization in visual mental imagery retrieval. The amplitude (Martín-Buro et al. 2020; Griffiths et al. 2021) and timing of alpha desynchronization (Michelmann et al. 2016; Martín-Buro et al. 2020) have been proposed as indices of the accumulation of memory strength, so both are potential mechanisms that could support the behavioral advantage of vividly encoded imagery (D'Angiulli et al. 2013). We hypothesized that high-vividness items, compared with low-vividness ones, would show one of the following patterns at retrieval: (i) an earlier time course of alpha desynchronization, reflecting a more rapid access to the encoded mnemonic information, (ii) an increase in alpha desynchronization, which would be reflected by a greater decrease in alpha power, and would indicate retrieval of more or stronger mnemonic information for high vivid items, or (iii) *both* an earlier and greater increase in desynchronization for items encoded as high in vividness.

Methods

Participants

Thirty-one participants between the ages of 18 and 35 ($M = 23.0$, $SD = 3.39$) were recruited through Duke University's Psychology Subject Pool and Interdisciplinary Behavioral Research Center. Participants provided informed consent and were either credited (1 per hour) or paid ($15 per hour) for their time, in accordance with a protocol approved by the Duke University Medical Center Institutional Review Board. Participants were all right-handed and had normal or corrected-to-normal vision with no history of neurological or psychiatric diseases. The study took approximately 90 min to complete and was preceded by a one-hour setup.

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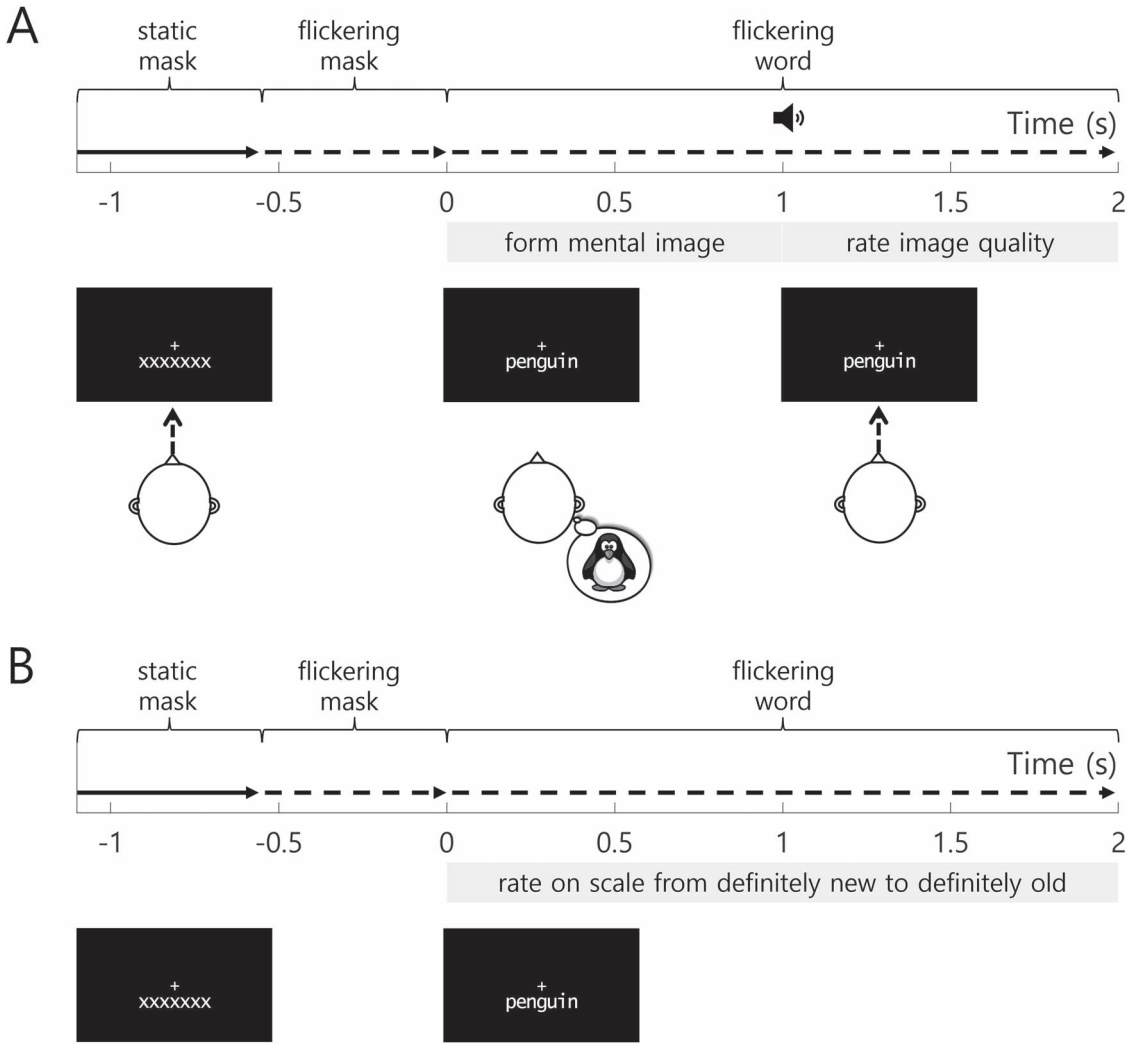

Fig. 1. Task paradigm. Participants were first presented with a mask stimulus, which was static for the first half of its presentation and flickering at 18 Hz for the second half. The mask stimulus was then immediately followed by a flickering object-word stimulus that was presented for 2 s. (A) During the encoding phase, participants were instructed to form a visual mental image for each word. One second after the onset of the word stimulus, they heard a tone indicating that they should rate the quality of the image they formed on a scale of 1 (poor/no image) to 4 (excellent). (B) During the retrieval phase, participants were instructed to identify the word as old or new and rate their confidence from 1 (definitely new) to 6 (definitely old). In this phase, they had the full 2 s to make their response.

Stimuli and procedure

Participants were seated 80 cm from a 24-inch stimulus presentation monitor (144-Hz refresh rate) in a dimly lit, electrically shielded room. The study consisted of an encoding phase (600 trials) and retrieval phase (900 trials), separated by a 5-min break. For both phases, participants maintained fixation on a white cross in the middle of a black screen. Stimulus presentation was controlled using Presentation 20.1 Software (Neurobehavioral Systems, Inc., Berkeley, CA). At the start of each trial, a static mask stimulus was presented just below the fixation cross for 555.6 ms. The mask consisted of a row of 5-7 lowercase Xs. After 555.6 ms, the mask began to flicker at 18 Hz for another 555.6 ms and was then replaced by a flickering 5-7 letter object-word or non-word stimulus for 2 s. Object-word stimuli appeared on 95% of trials and non-word stimuli on the remaining 5%. For consistency in visual input, the mask, object-word, and non-word stimuli were presented using a monospaced font (Lucida Console, size 24) and grouped so that all five-letter stimuli appeared in a row, followed by the six- and then seven-letter stimuli. There were an equal number of five-, six-, and seven- letter words.

During the encoding phase, participants were instructed to form a mental image of each object-word stimulus, with as much imagery detail as possible, for the first 1 s of the stimulus presentation. One second after the onset of the word stimulus, a tone was presented and participants had the remaining 1 s to rate the image vividness on a scale of 1 (poor/no image) to 4 (excellent image). Responses were made on a keyboard using their left hand. During the non-word stimulus trials, participants were instructed to just press the space bar with their left-hand thumb as quickly as possible. The non-word stimulus trials were included to encourage participants to maintain vigilant attention during the mask presentation because they required an immediate response after the offset of the mask stimulus, instead of needing to invoke any imagery processes and then wait for a tone before responding with a rating of the vividness of that imagery. The encoding phase took ~35 min to complete and consisted of five blocks (120 trials per block), with breaks in between each block.

The retrieval phase was a surprise to participants to ensure that encoding would be incidental. All 570 object-word stimuli from encoding were presented with an additional 285 new words

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and 45 new non-words. The trials were presented with the same procedure as the encoding phase, with the mask stimulus followed by either a word (95% of trials) or non-word stimulus. Again, the mask was presented statically for the first 555.6 ms and flickering for another 555.6 ms. Similarly, the word and non-word stimuli were presented flickering at 18 Hz for 2 s. However, in contrast to the encoding phase, there was no tone presented at any point during the retrieval phase. Participants were tasked with making a recognition response, rating each item on a scale from 1 (definitely new) to 6 (definitely old), thereby providing a combined memory and confidence judgment. On the non-word stimulus trials, participants again were instructed to respond by pressing the space bar as quickly as possible. The retrieval phase took ∼50 min to complete and consisted of five blocks (180 trials per block), with breaks in between the blocks. The stimuli were flickered in both the encoding and retrieval phases of the experiment so that the presentation would be matched/compatible across the phases. However, the flickering was only directly relevant in the analysis of the encoding phase, where we measured steady-state visual evoked potentials (SSVEPs) of the flickering as an index of internally-directed attention during visual mental imagery (Gjorgieva et al. 2022). In that analysis, the mask served as a baseline for the SSVEP. The current paper, in contrast, focuses on the analysis of the retrieval phase.

Behavioral data and analysis

Trials were excluded if participants responded within 150 ms of the onset of the word stimulus or if they failed to make a response. To evaluate general retrieval performance, participants' accuracy data were submitted to a one-way (confidence: low/medium/high) repeated-measures analysis of variance (rANOVA). Additionally, participants' RT data at retrieval were submitted to a 2 (memory: remembered/forgotten) × 3 (confidence: low/medium/high) rANOVA. As in our previous paper (Gjorgieva et al. 2022) that investigated the encoding of visual mental images, the vividness levels were established by binning trials into a High Vividness (*HighViv*) level and a Low Vividness (*LowViv*) level. The HighViv level included retrieval trials for items that had been rated at the highest vividness rating (4) at encoding, and the LowViv level included retrieval trials for items that had been rated at the two lowest vividness ratings (1 and 2) at encoding, which enabled trial counts for the two conditions to be relatively similar. HighViv and LowViv items were compared in terms of their RTs and confidence ratings at retrieval using paired-sample *t*-tests. For a more direct comparison of vividness, we also controlled for both memory accuracy and confidence by comparing RTs for high- and low-vividness items that were all successfully remembered with high-confidence (*HighViv-RemHighConf* and *LowViv-RemHighConf*).

EEG data acquisition and preprocessing

Online EEG data were recorded for both phases, and the data from the encoding phase have been previously reported (Gjorgieva et al. 2022). A custom, 64-channel, extended-coverage cap (Woldorff et al. 2002) was used with active electrodes (actiCAP, Brain Products GmbH) and an online right-mastoid reference. Impedences were maintained below 5 kOhms for the ground and mastoid electrodes and below 15 kOhms for the remaining electrodes. Data were digitized at 500 Hz per channel, with a three-stage cascaded integrator low-pass comb filter with a 130-Hz corner frequency. One electrode was positioned below the left eye for the vertical electrooculogram (EOG), and two electrodes were positioned lateral to the outer canthus of each eye for the horizontal EOG channel. These electrodes were used to monitor for blinks and horizontal eye movements.

Offline, the data were first filtered with a 40-Hz low-pass filter, then downsampled to 250 Hz, then filtered with a 0.1-Hz high-pass causal FIR filter, and finally re-referenced to the algebraic average of the left and right mastoid electrodes. Excessively noisy channels were interpolated using a spherical spline procedure (Perrin et al. 1989). The data were epoched from −2,750 to 3,750 ms, relative to the onset of the word or non-word stimuli. Eyeblinks that occurred near stimulus onset and could subsequently influence the initiation of the neural processing cascade were detected by submitting the data to an algorithm using a 150-ms wide window moving in 50-ms steps from −100 to 300 ms. Any epochs with peak-to-peak voltage differences that exceeded 40 μV in the vertical EOG channel were marked for rejection. We conducted an infomax independent component (IC) analysis on a copy of the EEG data that was epoched from −1,100 to 200 ms to avoid overlapping trials. The resulting component weights were transferred back to the original data set and ocular components reflecting eyeblinks were removed from the data (at most four per participant). Horizontal eye movements were detected by submitting data to an algorithm using a 150-ms moving window. The window moved across the epoch from −100 to 2,000 ms in 50-ms steps and marked for rejection the epochs with peak-to-peak voltage differences that exceeded 24 μV (corresponding to approximately 1.5° of eye movement) in the vertical EOG channel. The final data-cleaning procedure removed any high-amplitude noise or excess muscle activity. For this procedure, when three or fewer electrodes (excluding the vertical and horizontal EOG channels) exceeded ±100 μV for an epoch, each of these electrodes were replaced using the spherical-spline interpolation procedure. Alternatively, when more than three electrodes exceeded the threshold, the epoch was marked for rejection.

Eight participants were excluded due to > 70% of trials being rejected, either due to poor EEG data quality ($n = 5$), or a combination of both poor behavioral performance and poor EEG data quality ($n = 3$). This left 23 participants in the final analyses (15 female, mean age 22.5 years). The nonword-stimulus catch trials were also excluded from the final analyses. Data were preprocessed and analyzed in MATLAB with a combination of EEGLAB, ERPLAB (Lopez-Calderon and Luck 2014), and FieldTrip (Oostenveld et al. 2011). The EEG cap featured a custom-modified 10-10, equidistant electrode montage with extended inferior occipital coverage (Woldorff et al. 2002). Electrode sites in our montage are reported based on standard 10-10 electrode names for electrodes within 5 mm of the corresponding 10-10 site. If the electrodes were 5–10 mm from the 10-10 site, the name has a prime appended to it. If the electrodes were 10–15 mm from the 10-10 site, a subscript "a" was added for electrodes anterior to the listed 10-10 site, and a "p" was added for those posterior to the 10-10 site. No electrodes were further than ∼15 mm from their closest standard 10-10 site.

EEG and ERP analysis

For the ERP analysis, we examined the parietal old/new effect by selectively averaging trials that were time-locked to the onset of the word stimuli during the retrieval phase. Based on previous literature (Friedman and Johnson 2000; Woodruff et al. 2006; Wynn et al. 2019), we selected a cluster of electrodes that centered on Pz and included electrodes P1' and P2'. To investigate the effect of memory, we compared retrieval trials of old items that were successfully remembered (*Rem*) to retrieval trials of new items that were correctly identified as new (*CorrRej*). Trials in which participants rated their confidence at the lowest level were excluded,

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as their accuracy rate was near chance ($M = 56.8\%$). Mean amplitude data were submitted to a 2 (memory: Rem/CorrRej) × 4 (time: 400–500/500–600/600–700/700–800) rANOVA in 100 ms time bins, and Holm-adjusted post-hoc paired sample *t*-tests were conducted to identify any significant differences between the two conditions within each time bin. The time window was selected based on previous papers identifying the parietal old/new effect between 400 and 800 ms (Curran 2000; Curran and Cleary 2003). Similarly, to evaluate the effect of vividness (while controlling for memory and confidence), we focused only on retrieval trials for old items that were successfully remembered with high-confidence and subdivided them based on whether the items had been rated as high-vividness (*HighViv-RemHighConf*) or low-vividness (*LowViv-RemHighConf*) at encoding. Mean amplitude data were submitted to a 2 (vividness: HighViv-RemHighConf/LowViv-RemHighConf) × 4 (time: 400–500/500–600/600–700/700–800) rANOVA in 100-ms time bins. Holm-adjusted post-hoc paired sample *t*-tests were again conducted to identify significant differences between conditions within each time bin.

To ensure that the ERP results were distinct from the oscillatory results, the average ERP of each condition was subtracted out from the raw waveform on each trial that was in that condition. Then, frequency decomposition of the EEG was performed using multitaper methods that were based on discrete prolate spheroidal sequences to estimate power in logarithmically spaced frequencies ranging from 3 to 40 Hz. The taper window widths were 3 cycles for 3 Hz, 4 cycles for 4–7 Hz, 5 cycles for 8–14 Hz, 7 cycles for 15–20 Hz, and 10 cycles for 21–40 Hz. Spectral smoothing through multitapers was calculated as $5 \times \log_{10}$ of each frequency. We performed a decibel conversion to normalize and baseline the data relative to the static presentation of the mask stimulus (−848 to −600 ms relative to the onset of the word stimulus).

As noted above, the focus here was on the power changes in the alpha band (8-12 Hz). In particular, posterior alpha power was calculated as the average oscillatory activity between 8 and 12 Hz across a cluster of electrodes centered on electrodes Pz and POz, and including electrodes O1', O2', PO1, PO1, PO5, PO6, P3a, P4a, C5p, and C6p. To evaluate the effect of vividness, mean alpha power data were submitted to a 2 (vividness: HighViv-RemHighConf/LowViv-RemHighConf × 6 (time: 500–600/600–700/700–800/800–900/900–1,000/1,000–1,100) rANOVA in 100-ms time bins. Holm-adjusted post-hoc paired samples *t*-tests were conducted to identify time bins that differed significantly between conditions.

In addition to the amplitude analyses, we conducted latency analyses on the alpha-power time course. The time-point for the peak amplitude of the alpha was identified for each condition of interest on every subject searching from 0 to 1500 ms. We conducted paired samples *t*-tests to compare HighViv-RemHighConf and LowViv-RemHighConf trials.

Results

Behavioral results

We evaluated retrieval performance as measured by accuracy for correctly identifying old and new items. Participants correctly identified 83.6% of old items as old (SD = 10.8) and 71.7% of new items as new (SD = 13.0). We also compared accuracy for identifying old and new items based on the self-reported confidence levels. Data were submitted to a one-way ANOVA with three levels (confidence: low/medium/high), which showed a significant effect of confidence, $F(2, 40) = 76.15$, $p < 0.001$, $n_p^2 = 0.79$. We observed improved accuracy for higher-confidence items (low: $M = 56.8$, $SD = 0.06$, medium: $M = 73.8$, $SD = 0.14$, high: $M = 87.1$, $SD = 0.09$). Holm-adjusted post-hoc paired samples *t*-tests showed that accuracy was significantly higher for the high confidence compared with medium confidence items, $t(20) = -4.69$, $p_{Holm} < 0.05$, $d = -1.02$, as well as for the medium confidence compared with low confidence items, $t(20) = -6.35$, $p_{Holm} < 0.025$, $d = -1.39$. This analysis confirmed that the confidence levels were indicative of stronger memory. The trials with the lowest confidence level were excluded from subsequent analyses because their accuracy was near chance.

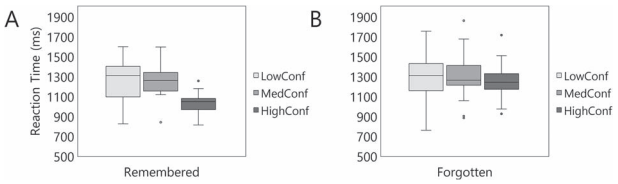

Fig. 2. RTs for memory retrieval. The left panel shows the mean and distribution of RTs for the successfully remembered old items split based on self-reported confidence levels. The right panel shows the mean and distribution of RTs for the forgotten old items divided by confidence level. Participants were fastest at making a response for items they remembered with high confidence. There was a significant difference between the items remembered with high confidence and all other categories. There were no significant differences amongst the other categories.

We assessed RTs at retrieval by comparing the levels of confidence (low, medium, and high) for remembered and forgotten items. The RT data were submitted to a 2 (memory: remembered/forgotten) × 3 (confidence: low/medium/high) rANOVA (Fig. 2). Results showed a significant effect of memory, $F(1, 16) = 18.96$, $p < 0.001$, $n_p^2 = 0.54$, indicating differences in RTs for remembered versus forgotten items. Additionally, there was a main effect of confidence, $F(2, 32) = 4.79$, $p = 0.02$, $n_p^2 = 0.23$, indicating a difference in RTs based on the self-reported level of confidence at retrieval. Most critically, there was an interaction between memory and confidence, $F(2, 32) = 15.41$, $p < 0.001$, $n_p^2 = 0.49$. Holm-adjusted post-hoc paired samples *t*-tests showed that this interaction was driven by a significant difference in RTs between high-confidence remembered items ($M = 1029$, $SD = 100$) and the rest of the conditions. More specifically, RTs were significantly faster for high-confidence remembered items than those remembered with medium-confidence ($M = 1267$ $SD = 170$; $t(15) = 4.32$, $p_{Holm} < 0.05$) and low-confidence ($M = 1276$, $SD = 191$; $t(15) = 4.65$, $p_{Holm} < 0.02$). Additionally, the items remembered with high-confidence had significantly faster RTs compared with items forgotten with high-confidence ($M = 1252$, $SD = 171$; $t(15) = 6.93$, $p_{Holm} < 0.01$), medium-confidence ($M = 1295$, $SD = 231$; $t(15) = 5.29$, $p_{Holm} < 0.013$), and low-confidence ($M = 1283$, $SD = 214$; $t(15) = 4.69$, $p_{Holm} < 0.017$). Taken together, the RT and accuracy results suggest that the high-confidence remembered items were remembered with the greatest fidelity and speed compared with the other categories.

Once we had a better understanding of the memory retrieval overall, we examined differences in memory retrieval for items that had been rated as high- versus low-vividness (*HighViv* and *LowViv*) at encoding by comparing accuracy, RTs, and confidence ratings for the two categories. Participants were more accurate at correctly identifying the old items that had been encoded with high-vividness ($M = 89.1$, $SD = 6.9$) compared with low-vividness ($M = 78.6$, $SD = 15.1$), $t(22) = 4.38$, $p < 0.001$, $d = 0.91$. Furthermore, we observed faster RTs at retrieval for the HighViv ($M = 1039$, $SD = 115$) compared with LowViv items ($M = 1113$, $SD = 135$), $t(22) = -8.16$, $p < 0.001$, $d = -1.70$ (Fig. 3A).

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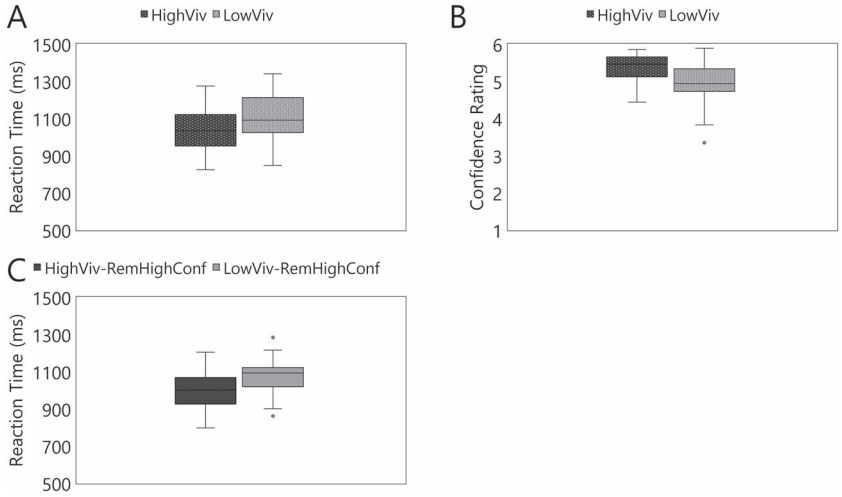

Fig. 3. RTs and confidence ratings for high-vividness compared with low-vividness items. (A) The mean and distribution of RTs at retrieval for items that had been rated as high- and low-vividness at encoding. Participants were faster at rating their confidence in their memory judgment for the high-vividness items. (B) The mean and distribution for confidence levels at retrieval ranging from 1 (definitely new) to 6 (definitely old). Participants were more confident when identifying items that had been rated as high-vividness at encoding. (C) The mean and distribution of RTs at retrieval for the items successfully remembered with high confidence as a function of image vividness at encoding. Controlling for both memory and confidence, we observed faster RTs for the high-vividness items that had been successfully remembered with high-confidence compared with the low-vividness items that had also been successfully remembered with high-confidence.

The confidence ratings ranged from 1 (definitely new) to 6 (definitely old). A "1" rating for an old item would indicate that the participant incorrectly identified the old item as new and were highly-confident, whereas a "6" rating would indicate that the participant correctly identified the old item as old with high confidence. Participants reported higher and more accurate confidence ratings for the HighViv ($M = 5.40$, $SD = 0.35$) over LowViv items ($M = 4.91$, $SD = 0.60$), $t(22) = 5.27$, $p < 0.001$, $d = 1.10$ (Fig. 3B). To minimize the influence of confidence, we limited the comparison of high- and low-vividness items to only items that were successfully remembered with high confidence (*HighViv-RemHighConf* vs. *LowViv-RemHighConf*). Again, results showed faster RTs for the HighViv-RemHighConf items ($M = 996$, $SD = 96$) compared with LowViv-RemHighConf ($M = 1071$, $SD = 98$), $t(22) = -11.86$, $p < 0.001$, $d = -2.47$ (Fig. 3C). This finding confirmed that the vividness-related RT difference was not accounted for just by differences in confidence. For a comparison of vividness levels that includes medium as well (*MedViv-RemHighConf*), see Figure S1 in the supplementary material.

ERP results

For the EEG analysis, our first goal was to examine episodic memory retrieval via the parietal old/new ERP effect. Based on prior research finding a modulation of the parietal old/new effect due to memory (Rugg and Curran 2007), we expected an increase in magnitude for the remembered old items compared with the new items that were correctly identified as new. To examine these differences based on memory, ERP data were submitted to a 2 (memory: Rem/CorrRej) × 4 rANOVA (time: 400–500 ms/500–600 ms/600–700 ms/700–800 ms). The results indicated a main effect of memory, $F(1, 22) = 9.17$, $p = 0.006$, $n_p^2 = 0.29$, and a significant main effect of time, $F(3, 66) = 11.58$, $p < 0.001$, $n_p^2 = 0.35$. Additionally, there was a significant interaction between these two factors, $F(3, 66) = 5.81$, $p = 0.001$, $n_p^2 = 0.21$, indicating the effect of memory differed as a function of time. Fig. 6(A) displays the mean amplitude and within-subject standard error for each time bin. Holm-adjustedpost-hoc paired samples *t*-tests showed an increased magnitude (larger positivity) for the successfully

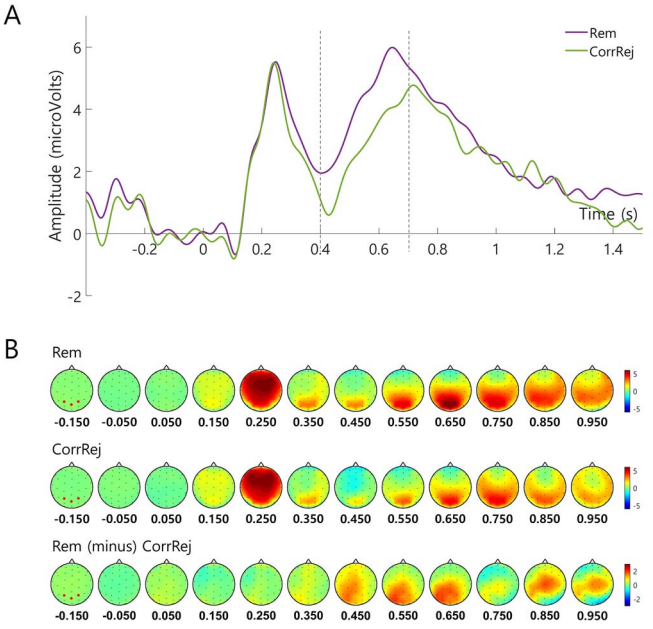

Fig. 4. Effect of memory on the parietal old/new ERP effect. (A) Timelock-averaged data relative to the onset of the word stimulus during a retrieval trial. Results showed significant differences between the items successfully remembered and items successfully identified as new between 400 and 700 ms (indicated by the vertical dashed lines), with an increased magnitude for the remembered items. (B) The topographic plots show the trial time-course of each condition in 100-ms time bins. Each bin is labeled with the middle time point of the 100-ms period.

remembered items compared with the correctly identified new items between 400 and 700 ms (Fig. 4). Table 1 displays the means and standard deviations for each condition, as well as the results of the post-hoc *t*-tests for each time bin.

More critical to our research question, we wanted to examine differences based on vividness in the parietal old/new effect while controlling for memory accuracy and confidence. We hypothesized that if the high-vividness items were remembered with greater fidelity, we would observe an increased magnitude

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Table 1. Post-hoc paired samples *t*-tests comparing Rem and CorrRej ERP activity across time.

	Rem mean (SD)	CorrRej mean (SD)	*t*	df	p_{Holm}	*d*
400–500 ms	2.41 μV (3.92)	1.18 μV (4.53)	3.59	22	<.017*	.75
500–600 ms	4.38 μV (4.66)	2.85 μV (4.46)	3.88	22	<.013*	.81
600–700 ms	5.70 μV (4.44)	4.08 μV (4.33)	3.25	22	<.025*	.68
700–800 ms	4.78 μV (3.95)	4.46 μV (3.96)	.63	22	.539	.13

Note: * indicates significant differences

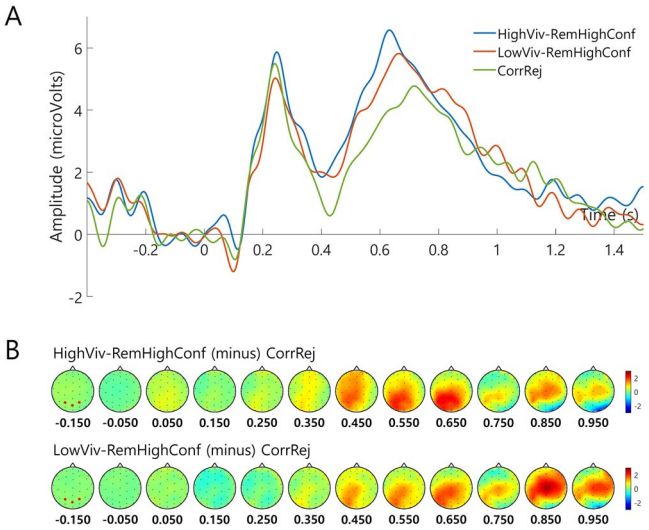

Fig. 5. Effect of vividness on the parietal old/new ERP effect. (A) Timelock-averaged data comparing the effect of the vividness rating at encoding during memory retrieval for items remembered with high confidence. Findings showed no significant differences on this retrieval ERP effect for items that had been encoded with high-vividness compared with those that had been encoded with low-vividness. (B) The topographic plots show the time-course for each condition in 100-ms time bins, each labeled with the middle time point of the period.

in the parietal old/new effect in comparison with the low-vividness items. We calculated the difference waves for the HighViv-RemHighConf and LowViv-RemHighConf items relative the correctly rejected new items by subtracting the CorrRej ERP from both HighViv-RemHighConf and LowViv-RemHighConf. The difference wave data were submitted to a 2 (memory: HighViv-RemHighConf/LowViv-RemHighConf) × 4 (time: 400–500/500–600/600–700/700–800 ms) rANOVA. Unlike the comparison based on memory, the results of this analysis showed no main effect of vividness on this ERP effect, $F(1, 22) = 1.13$, $p = 0.299$, $n_p^2 = 0.05$. We did observe a main effect of time, $F(3, 66) = 4.83$, $p = 0.004$, $n_p^2 = 0.18$, but importantly, there was no interaction, $F(3, 66) = 1.42$, $p = 0.245$, $n_p^2 = 0.06$. There were no differences in the parietal old-new ERP effect when comparing high- and low-vividness items that had been remembered with high confidence (Fig. 5). Table 2 displays the means and standard deviations for each condition, and Fig. 6(B) displays the mean amplitude and within-subject standard error for each time bin. Our findings suggest that high- and low-vividness items were retrieved fairly equivalently, at least as reflected by the parietal old/new effect. In the supplemental material, we confirm that there are no differences between the vividness levels when we also include medium vividness into the analysis (see Table S1 and Fig. S2).

Oscillatory results

Based on previous research identifying parietal alpha as an index of memory strength at retrieval (Griffiths et al. 2019; Martín-Buro et al. 2020), we evaluated the effects of vividness at

Table 2. Mean and standard deviations of HighViv-RemHighConf [MINUS] CorrRej and LowViv-RemHighConf [MINUS] CorrRej difference waves across time.

	HighViv-RemHighConf [MINUS] CorrRej Mean (SD)	LowViv-RemHighConf [MINUS] CorrRej Mean (SD)
400–500 ms	1.30 μV (.44)	.95 μV (.40)
500–600 ms	1.77 μV (.50)	1.18 μV (.53)
600–700 ms	2.06 μV (.68)	1.40 μV (.60)
700–800 ms	.49 μV (.64)	.47 μV (.52)

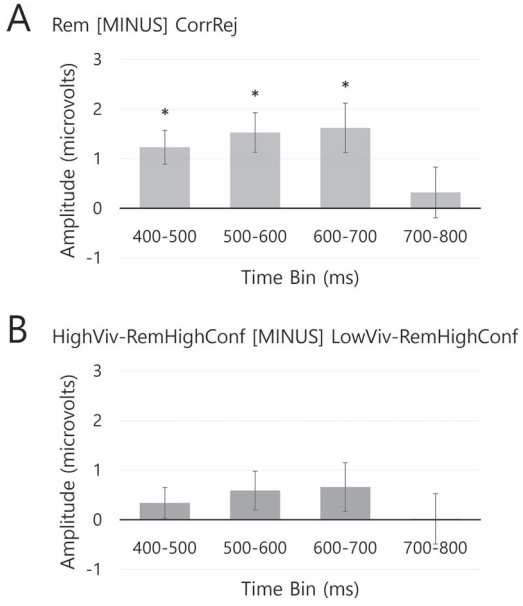

Fig. 6. Within-subject differences for the parietal old/new effect. (A) The Rem minus CorrRej calculation for the parietal old/new effect within each time bin with error bars indicating the within-subject standard error. The asterisk indicates significant differences. (B) The difference between HighViv-RemHighConf and LowViv-RemHighConf was calculated for the parietal old/new ERP within each time bin. Error bars indicate the within-subject standard error. There were no significant differences between the conditions in this ERP activity.

retrieval by comparing the HighViv-RemHighConf and LowViv-RemHighConf items. For the amplitude analysis, data were submitted to a 2 (vividness: HighViv-RemHighConf/LowViv-RemHighConf) × 6 (time: 500–600/600–700/700–800/800–900/900–1,000/1,000–1,100 ms) rANOVA. Fig. 7(A) displays the time-course and (B) displays the topography of alpha power at retrieval for the HighViv-RemHighConf and LowViv-RemHighConf items. Our results showed no main effect of vividness across the total analyzed time period, $F(1, 22) = 0.44$, $p = 0.513$, $n_p^2 = 0.02$, and a weak trending main effect of time, $F(5, 110) = 1.92$, $p = 0.097$, $n_p^2 = 0.08$. However, we observed a significant interaction of these two factors, $F(5, 110) = 11.87$, $p < 0.001$, $n_p^2 = 0.35$, indicating that

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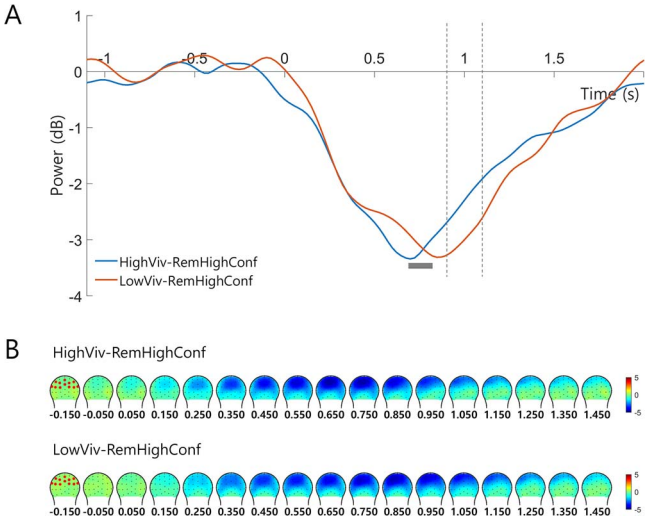

Fig. 7. Effect of vividness on alpha power when controlling for confidence. (A) Timelock-averaged parietal alpha power plotted over the time-course of a retrieval trial, with the onset of the word stimulus occurring at time 0. Results showed a significant difference between 900 and 1,100 ms (indicated by the vertical dashed lines). Moreover, we observed a significant difference in the latency of the alpha effect, whereby the high-vividness items remembered with high confidence were represented by a faster decrease in alpha power compared with the low-vividness items remembered with high confidence. (B) The topographic plots show the time-course of the trial for each condition in 100-ms time bins. Each bin is labeled with the middle time point for each 100-ms period.

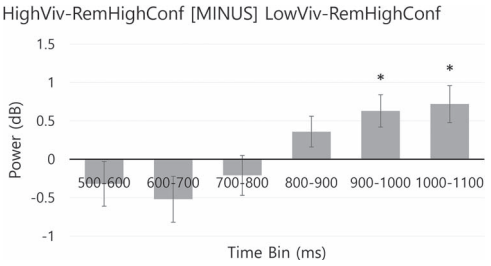

Fig. 8. Within-subject differences for alpha. The HighViv-RemHighConf minus LowViv-RemHighConf difference within each time bin for the alpha power. Error bars indicate the within-subject standard error, with * indicating significant differences.

the effects on the magnitude differed across the time bins for high-vividness versus low-vividness items. Fig. 8(B) displays the mean amplitude and within-subject standard error for each time bin. Holm-adjusted post-hoc paired samples *t*-tests comparing the low- and high-vividness items showed a significant difference between 900 and 1,100 ms, with decreased alpha power for the low-vividness items during these periods. Table 3 displays the means and standard deviations for each condition and the *t*-test results at each time bin. Importantly, it can be seen that these significant differences in alpha power were accompanied by an apparent difference in latency, with an earlier latency of the decrease in alpha power for the high-vividness items. Accordingly, we conducted an analysis on the latency of alpha as well.

For the peak latency analysis, we hypothesized that the HighViv-RemHighConf items would have a faster latency of the alpha effect at retrieval, in line with the theory suggesting faster access to sensory memory traces for high-vividness items (D'Angiulli et al. 2013). We compared the peak amplitude latencies for the HighViv-RemHighConf and LowViv-RemHighConf items using a paired samples *t*-test. In line with our hypothesis, we observed a faster latency of the negative peak of the alpha power time course for the high-vividness ($M = 679$, $SD = 182$) compared with low-vividness ($M = 821$, $SD = 200$) items, $t(22) = -2.96$, $p = 0.007$, $d = -.62$. These neural findings suggest that the high-vividness items were retrieved more quickly than the low-vividness items, consistent with the faster RTs that followed. This faster retrieval of the high-vividness items then ramifies into the difference in amplitude that we observed afterwards. More specifically, the retrieval process begins and concludes more quickly for the high-vividness items than for the low-vividness items, even though they all are remembered with high confidence. In the supplemental material (see Table S2 and Fig. S3), we extend these analyses to the full vividness spectrum (including medium vividness) and find that the speed boost is specific to the high-vividness items. There is no boost in retrieval speed for the medium vividness items relative to low-vividness.

Discussion

In this study, subjects were asked to generate visual mental images of a series of object words and rate the vividness of those images. After the generation of this series of mental images, subjects completed a surprise old/new recognition task, which included rating their memory confidence. Using this paradigm, we replicated the alpha power decrease for successfully remembered items (Martín-Buro et al. 2020) and the decreased RT for high-vivid encoded items (D'Angiulli et al. 2013). We also provided new neural evidence indicating that items that were imaged with high-vividness at encoding produce an earlier decrease in alpha-band activity at retrieval compared with low-vividness ones. This result links previous behavioral research about mental imagery (Yi et al. 2008; D'Angiulli et al. 2013) with neural research about alpha-band desynchronization and memory-retrieval processes (Naselaris et al. 2011; Pearson et al. 2015; Koenig-Robert and Pearson 2019). Previous studies have investigated the neural regions associated with the generation of mental imagery (O'Craven and Kanwisher 2000; Kosslyn and Thompson 2003; Lee et al. 2012; Pearson et al. 2015) and their modulation according to the vividness of that image (Dijkstra et al. 2017). However, to our knowledge, this is the first study to investigate the neurophysiological measures of the retrieval of previously-encoded mental images, in particular as a function of the vividness of those images at encoding.

Modulations in alpha-band oscillations have been found to play a widespread role in human cognition (Hanslmayr et al. 2009; Başar 2012; Klimesch 2012; Obleser and Weisz 2012), including their particular influence on memory functions. In a recent study, Martín-Buro et al. (2020) asked participants to encode pairs of words, perform an old/new recognition task for one word from the pair and then recollect the associated word. They showed that alpha desynchronization increased across the different memory performances (new < old < associated word). More generally, this effect has been seen in an association between both alpha and beta band desynchronization, reflecting the amount of information retrieved from episodic memory (Khader and Rösler 2011; Hanslmayr et al. 2016; Griffiths et al. 2019; Martín-Buro et al. 2020). This relationship has been interpreted as modulations in alpha/beta band activity promoting the information flow to the neural substrates that represent mnemonic content (Klimesch et al. 2007; Hanslmayr et al. 2012; Hanslmayr et al. 2016).

In this study, we observed that items remembered with high confidence that had been rated as highly-vivid during the image generation process at encoding, had an earlier negative peak in

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Table 3. Post-hoc paired samples *t*-tests comparing HighViv-RemHighConf and LowViv-RemHighConf alpha power across time.

	HighViv-RemHighConf Mean (SD)	LowViv-RemHighConf Mean (SD)	*t*	df	p_{Holm}	*d*
500–600 ms	−2.82 dB (1.41)	−2.53 dB (1.33)	−1.00	22	.327	−.21
600–700 ms	−3.21 dB (1.51)	−2.75 dB (1.38)	−1.61	22	.122	−.34
700–800 ms	−3.24 dB (1.44)	−3.07 dB (1.34)	−.63	22	.536	−.13
800–900 ms	−2.89 dB (1.37)	−3.28 dB (1.17)	2.00	22	.058	.42
900–1,000 ms	−2.53 dB (1.49)	−3.17 dB (1.25)	3.10	22	<.008*	.65
1,000–1,100 ms	−2.14 dB (1.49)	−2.87 dB (1.41)	3.05	22	<.01*	.64

Note: * indicates a statistically significant difference

alpha oscillations during retrieval compared with mental images that had been rated as low-vivid at encoding but had also been remembered with high confidence. This shifted time course of alpha desynchronization can be interpreted as an earlier memory reinstatement (Hanslmayr et al. 2012; Hanslmayr et al. 2016; Griffiths et al. 2019) for the high-vividness items. This result, therefore, provides the first neural evidence in support of the theory from D'Angiulli et al. (2013), based on multiple memory-trace theory (Moscovitch et al. 2016), which postulates that higher vividness is reflective of a greater availability of multiple memory traces in long term memory, thereby enabling both faster image generation and faster retrieval. This latency difference also ramified into an amplitude difference in alpha power from 900 to 1,100 ms, as the retrieval process began and completed earlier in time for the high-vividness items.

Our results showed no differences in the magnitude of the parietal old/new ERP effect when comparing the high-vividness to low-vividness items. As we compared high- and low-vividness items that had all been successfully remembered with high-confidence, it stands to reason that there would be no significant differences in memory strength between the high- and low-vividness items. This could be due to differential encoding-related processes leading to equivalent memory strength at retrieval. In our previous paper (Gjorgieva et al. 2022) analyzing the encoding phase of this experiment, we observed that participants needed a more sustained level of internally-directed attention (as indexed by the steady-state visual evoked potentials that were recorded) to generate low-vividness images that could be successfully later remembered. Additionally, in that study subjects showed a more sustained Dm ERP effect for the subsequently remembered low-vividness items, compared with the remembered high-vividness items, suggesting conceptual processing may have been used to compensate for the low-vividness of the mental images at encoding.

However, our latency findings suggest that even when low-vividness items are retrieved with high confidence, the speed of that memory reinstatement is still slower than the reinstatement for the high-vividness items. Relatedly, a study by Voss et al. (2010) found that perceptual priming repetition effects were observed early in the ERP response, as reflected by the P170 ERP component, whereas conceptual priming repetition effects were observed at longer latencies as reflected by the FN400 ERP. This may point to a similar mechanism whereby perceptual processing at encoding (occurring in the mind's eye during mental imagery) can be accessed more quickly at retrieval in comparison to conceptual processing that occurred at encoding. Future research is needed to gain further understanding of the neural underpinnings of the vividness-sensitive retrieval processes, as well as other cognitive processes that may help compensate for lower imagery vividness.

We note that our study had some important limitations. Peak latency measures the time at which a peak reaches its maximum (or here minimum) value. Latency measures of electrophysiologically based waveforms tend to be noisier than mean amplitude measures. However, we note that we are applying peak latency to waveform data that was smoothed during the spectral decomposition process, which should eliminate much of the noise in the signal, and our findings clearly support a significant latency difference in the alpha-power changes. Nevertheless, more studies are needed to further assess the differences in latency observed in this study. Additionally, our study used a recognition task as a measure of retrieval processes. Future research is needed to assess whether these findings extend to other episodic retrieval mechanisms, such as free or cued recall.

In summary, the current study shows that items that were generated with high-vividness at encoding are retrieved from memory more quickly than low-vividness items, even for items that are all remembered with high confidence, and that this process is indexed neurally by the speed of alpha-band desynchronization during that retrieval. Accordingly, such results provide an important link between the memory retrieval literature and the visual mental imagery literature.

Author contributions

Eva Gjorgieva (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Validation, Visualization, Writing—original draft, Writing—review and editing), Ricardo Morales Torres (Writing—original draft, Writing—review and editing), Roberto E Cabeza (Conceptualization, Resources, Software, Supervision, Writing—review and editing), Marty Woldorff (Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Visualization, Writing—original draft, Writing—review and editing).

Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

Conflict of interest statement: None declared.

Data availability

The authors will supply the relevant data in response to reasonable requests.

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