

Running title: WORKING MEMORY BOOSTS LONG-TERM MEMORY RETRIEVAL


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Working memory processing boosts the neural representation of long-term memories

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Abstract

Understanding the interaction between short-term and long-term memory systems is essential for advancing our knowledge of human memory. This study investigates whether working memory processes, specifically attentional prioritization (Experiments 1 and 2) and testing (Experiment 2), can enhance the neural activity associated with recently encoded long-term memories. A total of 86 participants completed a novel three-phase memory task that integrated a traditional long-term memory learning task with a working memory paradigm. In the first phase, participants encoded object-location associations. During the second phase, these associations were reintroduced in a working memory task that manipulated attentional prioritization; participants were required to report the location of the cued object. In the final phase, participants recalled the locations associated with each object. By analyzing both behavioral performance and electroencephalogram (EEG) data collected during this retrieval phase, we found that attentional prioritization in working memory significantly improved long-term memory retrieval, a finding supported by corresponding neural evidence. Additionally, Experiment 2 demonstrated that both prioritization and testing in working memory jointly enhance the neural representation of long-term memories. These findings indicate that working memory processes can dynamically alter the neural patterns underlying long-term memory representations, revealing a more integrated role for working memory in long-term memory consolidation.

Keywords: *long-term memory, working memory, attentional prioritization, retro-cue paradigm, EEG, event-related potentials, decoding*

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1. Introduction

2 Understanding the dynamic interplay between our short-term and long-term memory systems
3 is essential in the pursuit of understanding human memory and learning. Already in the 1960s,
4 theories proposed by Atkinson and Shiffrin suggested a continuous interaction between these
5 memory systems¹. These ideas remain influential in contemporary memory research. For
6 instance, Cowan and colleagues propose a simultaneous information exchange between
7 working-and long-term memory. Accordingly, information in working memory activates long-
8 term memory representations^{2,3}, while retrieved long-term memory content is temporarily
9 maintained in working memory⁴. Likewise, Oberauer and colleagues discuss the existence of
10 a flexible gate mechanism that regulates the entry of long-term memory content into working
11 memory, allowing it only when beneficial⁵⁻⁸. This reciprocal exchange underscores the active
12 role of working memory in shaping and accessing long-term memory representations.

13 Previous research has extensively explored how various maintenance and manipulation
14 processes in working memory affect the transfer of information to long-term memory and its
15 subsequent recall. A key phenomenon in this area is the McCabe effect, which shows improved
16 long-term recall for words interrupted by an arithmetic task during working memory
17 maintenance compared to uninterrupted words (complex vs. simple span tasks)⁹. This
18 improvement is attributed to the covert retrieval of words during the maintenance period while
19 solving the arithmetic task⁹⁻¹¹ (for conflicting evidence obtained in experiments using complex
20 stimuli, see¹²). Other explanations include benefits from the extended time spent in working
21 memory^{13,14} or elaboration during the maintenance period¹⁵.

22 Studies on the transfer of information between working memory and long-term memory
23 have also examined the role of attentional processes. Depending on their operationalization,
24 researchers have assessed how attentional refreshing, value-based attentional prioritization,
25 and cue-based attentional prioritization in working memory affect information transfer to long-

1 term memory and subsequent retrieval. Attentional refreshing, which involves briefly thinking
2 about a recently encountered stimulus to reactivate its representation¹⁶, shows mixed evidence
3 regarding its benefit for delayed long-term memory recall. Some studies suggest that attentional
4 refreshing in working memory leads to enhanced long-term memory retrieval^{17,18}, while others
5 do not find such benefits¹⁹ beyond simple repetition²⁰. In contrast, the effects of attentional
6 prioritization on long-term memory retrieval depend on the type of cue. Cue-based attentional
7 prioritization in working memory has been linked to enhanced long-term recall²¹⁻²⁵, whereas
8 reward-cue-based prioritization was not associated with such long-term benefits^{25,26}. These
9 findings suggest that the operationalization of attentional processes matters when studying
10 long-term memory recall benefits, with cue-based attentional prioritization proving to be the
11 most robust effect.

12 The studies described above consistently examined how attentional processes in
13 working memory impact the transfer of information from short-term to long-term memory.
14 However, an important yet unanswered question is whether these working memory processes
15 can also enhance *existing* long-term memory representations that have been recently encoded
16 but not yet consolidated. This question is crucial because evidence of such an effect would
17 suggest that working memory not only facilitates the transfer of information to long-term
18 memory but also actively modifies and strengthens existing representations. This implies a
19 more dynamic and flexible relationship between working memory and long-term memory than
20 previously thought. Instead of merely acting as a temporary buffer, working memory could also
21 serve as an instance, in which long-term memories are further manipulated and reinforced.
22 These findings would significantly expand our understanding of the interaction between these
23 two memory systems.

24 In Experiment 1, we examined the extent to which cue-based attentional prioritization
25 in working memory enhances the retrieval of previously encoded long-term memory

1 representations. We investigate this effect not only behaviorally, but also at the neural level via
2 the parietal old-new effect, an established EEG component of long-term memory
3 recollection^{27–31}. To foreshadow the results of Experiment 1, we found that both behavioral and
4 EEG data supported enhanced long-term memory retrieval of information undergoing cued-
5 based attentional prioritization in working memory.

6 To determine whether the observed effect is due solely to attentional prioritization or a
7 combination of attentional prioritization and testing effects in working memory, we conducted
8 Experiment 2. Both behavioral and neural evidence revealed that, compared to a control
9 condition, items that were either prioritized or tested in working memory showed enhanced
10 long-term memory retrieval. Similarly, EEG results suggested that both attentional
11 prioritization and testing in working memory enhance long-term memory representations and
12 their retrieval. Importantly, accuracy data revealed a distinct benefit for attentional
13 prioritization over testing, a difference not reflected at the neural level. Overall, findings are
14 discussed in light of attentional prioritization and testing in working memory *jointly*
15 contributing to the enhancement of long-term memory representations and their subsequent
16 retrieval. Finally, we discuss the theoretical implications of these results for existing theories
17 describing the relationship between long-term- and working memory.

18 **2. Results**

19 In Experiment 1 participants completed a combined episodic long-term and working memory
20 task with three phases (see Figure 1a and b). In the first phase, they learned object-location
21 associations with the instruction to remember them for later recall. In the second phase, a
22 working memory (retroactive cuing / retro-cue) paradigm was introduced. Participants were

23 ##### Figure 1 #####

24 shown objects from the first phase, presented on their learned locations, along with two task-
25 irrelevant scrambled objects. Participants' task was to memorize the objects for a subsequent

1 test. After a short maintenance period, a 100% informative retro-cue indicated which object
2 would be tested. During test, participants had to decide if the cued object matched a centrally
3 presented object (i.e., probe). Each object appeared four times on the same location during the
4 working memory task. In the final retrieval phase, participants were shown all objects from the
5 first phase and were asked to report the location learnt in the first phase using a response device
6 with four spatially aligned buttons corresponding to the four possible locations (see Figure 1b).
7 All analyses were conducted on data from this third, long-term memory retrieval phase.
8 Notably, for our analysis these trials were sorted based on the processing that occurred during
9 the working memory task (i.e., the second phase), which determined the experimental condition
10 (for an overview, of the conditions, see Figure 1c).

11 Experiment 1 includes three experimental conditions based on how objects were
12 processed in working memory (or if they were excluded from such processing): (i) the
13 *prioritization condition*, involves attentional prioritization and testing of the previously
14 encoded long-term memory representation in working memory; (ii) the *non-prioritization*
15 *condition*, includes a brief presentation and maintenance of the object followed by the item
16 being placed outside the focus of attention, as it is no longer relevant for the subsequent
17 working memory test (also analogous to a repetition effect); and (iii) *absent in working memory*
18 (control) *condition*, in which the object is initially encoded into long-term memory and
19 retrieved in the last phase, but does not appear in the working memory task.

20 According to our hypothesis, if attentional prioritization in working memory enhances
21 *existing* long-term memory representations that have been recently encoded but not yet
22 consolidated, we should observe improved behavioral performance and a stronger parietal old-
23 new effect²⁷⁻³¹ in the prioritization compared to the non-prioritization and absent in working
24 memory condition. This would suggest that cue-based attentional prioritization in working

1 memory has the capacity to enhance the recall of long-term memories and that this effect goes
2 beyond simple repetition within working memory (non-prioritization condition).

3 **2.1. Long-term memory accuracy is boosted by attentional prioritization in working** 4 **memory – evidence from Experiment 1**

5 Table 1 shows the average retrieval phase accuracy, indicating that participants were most
6 accurate in the prioritization condition, followed by the non-prioritization condition, and least
7 accurate in the absent in working memory condition. Statistical comparisons using repeated
8 measures ANOVA (rm-ANOVA) revealed that sphericity was violated ($\chi^2(42) = 7.58, p = .02,$
9 $\epsilon = 0.85$), so Greenhouse–Geisser corrected results are reported. The accuracy analysis showed
10 a main effect of condition: $F(2, 84) = 51.85, p_{corr} < .001, \eta_p^2 = 0.55, BF_{10} = 1.98 \times 10^{12}$, with
11 the Bayes factor indicating very strong evidence in favor of the alternative hypothesis (see
12 Figure 2a). The Bayes factor of the post-hoc analyses revealed very strong evidence for the
13 accuracy difference between: (i) the prioritization vs. non-prioritization condition: $t(42) = 6.51,$
14 $p_{adj} < .001, d_{av} = 0.70, 95\% \text{ CI } [7.29, 13.83], BF_{10 \text{ corr}} = 116301.91$; (ii) the prioritization vs.
15 absent in working memory condition: $t(42) = 8.68, p_{adj} < .001, d_{av} = 1.05, 95\% \text{ CI } [12.10,$
16 $19.44], BF_{10 \text{ corr}} = 9.13 \times 10^7$; (iii) the non-prioritization vs. absent in working memory
17 condition: $t(42) = 4.19, p_{adj} < .001, d_{av} = 0.29, 95\% \text{ CI } [2.70, 7.72], BF_{10 \text{ corr}} = 104.60$. These
18 results indicate that cued attentional prioritization in working memory led to an increase in
19 long-term memory accuracy, surpassing performance for both items that were absent in the
20 working memory task and those that were merely presented (but never tested) in the working
21 memory task.

22 ##### Table 1 #####

23 ##### Figure 2 #####

24 **2.2. Decreased response times during long-term memory retrieval for prioritized items in** 25 **working memory – evidence from Experiment 1**

1 Descriptive analysis (see Table 1) showed that response times in the long-term memory
2 retrieval phase followed the same pattern as accuracy: participants were fastest for items that
3 appeared in the prioritization condition during the working memory task, followed by the non-
4 prioritization condition, and slowest in the absent in working memory condition. A comparable
5 repeated measures ANOVA (rm-ANOVA) was conducted to compare response times across
6 conditions. Since sphericity was violated ($\chi^2(42) = 14.03, p < .001, \epsilon = 0.77$), Greenhouse–
7 Geisser corrected results are reported. Results of the rm-ANOVA indicated a main effect of
8 condition: $F(2, 84) = 27.32, p_{corr} < .001, \eta_p^2 = 0.39, BF_{10} = 1.17 \times 10^7$, with the Bayes factor
9 indicating very strong evidence in favor of the alternative hypothesis (see Figure 2b). The
10 Bayes factor of the post-hoc analyses suggested very strong evidence for the response times
11 difference between: (i) the prioritization vs. non-prioritization condition: $t(42) = -5.23,$
12 $p_{adj} < .001, d_{av} = 0.33, 95\% \text{ CI } [-146.89, -65.12], BF_{10 \text{ corr}} = 2213.76$; and (ii) the prioritization
13 vs. absent in working memory condition: $t(42) = -5.89, p_{adj} < .001, d_{av} = 0.45, 95\% \text{ CI } [-195.21,$
14 $-95.62], BF_{10 \text{ corr}} = 16866.52$. The response times difference between the non-prioritization vs.
15 absent in working memory condition was only supported by weak evidence: $t(42) = -2.64,$
16 $p_{adj} = .01, d_{av} = 0.11, 95\% \text{ CI } [-69.53, -9.29], BF_{01 \text{ corr}} = 2.06$. Overall, similar to the accuracy
17 results, the response times pattern also confirms that cued prioritization is associated with faster
18 responses, which exceed the benefits observed when the item is either absent from working
19 memory or briefly presented and maintained during the working memory task.

20 **2.3. Enhanced parietal old-new component for prioritized items in working memory –** 21 **evidence from Experiment 1**

22 In addition to the behavioral measures, we investigated whether modulations of the parietal
23 old-new effect mirrored the observed behavioral patterns. This event-related potential
24 component is typically measured in tasks requiring old (previously encountered) versus new
25 (never encountered) decisions during memory retrieval and has been argued to reflect the

1 conscious recollection of long-term memories^{28,30–32}. Previous research has also shown that
2 this component can be differentially modulated by the retrieval of deeply versus superficially
3 encoded information²⁹ or by the retrieval of information with varying precision levels³³. As
4 indicated in Figure 2c, data from the electrode cluster P1, P3, P5³⁴ was averaged and contrasted
5 between conditions via cluster-based permutation statistics. Our analysis revealed a significant
6 cluster between 496-652 ms for the prioritization vs. non-prioritization contrast and a cluster
7 between 436-660 ms for the prioritization vs. absent in working memory condition contrast.
8 No statistically reliable effects were found when the non-prioritization and absent in working
9 memory condition were compared. These results indicate an enhanced long-term memory
10 retrieval for the object-location associations that underwent attentional selection in working
11 memory compared to the other two conditions.

12 **2.4. Overview of Experiment 2**

13 As outlined in the Introduction, Experiment 2 aimed to determine whether the effects observed
14 in Experiment 1 were due solely to attentional prioritization or also to testing effects in working
15 memory. We define the testing effect in this context as the extended, non-selective maintenance
16 of information in working memory to generate a response during the final match-no-match test.
17 However, for brevity, we will use the term “testing or testing effect”. To disentangle attentional
18 prioritization from testing effects, we introduced a new type of cue in the working memory
19 task: uninformative/neutral cues. Similar to Experiment 1, participants encoded the stimulus
20 display and were probed in a match-no-match task at the end of the trial. However, unlike
21 informative cues, neutral cues did not provide information about the to-be-tested item,
22 requiring participants to maintain both objects for the comparison in the working memory test.
23 Importantly, similar to Experiment 1, participants did not report any locations during the
24 working memory task. All other aspects were kept consistent with Experiment 1.

1 As illustrated in Figure 1c, Experiment 2 assumes that objects in the *prioritization*
2 *condition* undergo both attentional prioritization and testing in working memory. In contrast,
3 objects in the *testing condition* undergo a non-selective maintenance and testing at the end of
4 the trial. By comparing the final long-term memory retrieval of objects between these two
5 conditions, we can determine whether the benefits observed in Experiment 1 are due solely to
6 attentional prioritization or a combination of attentional prioritization and testing. The other
7 two conditions (*non-prioritization in working memory* and *absent in working memory*) are
8 identical to Experiment 1. According to our hypothesis, if long-term memory performance and
9 the amplitude of the parietal old-new component are higher in the prioritization condition
10 compared to the testing condition (with both differing from the absent in working memory
11 condition and non-prioritization condition), it would suggest that attentional prioritization
12 provides an additional long-term memory benefit beyond testing.

13 **2.5. Long-term memory accuracy is boosted by attentional prioritization above and** 14 **beyond testing in working memory – evidence from Experiment 2**

15 At a descriptive level (see Table 2), participants were the most accurate in the prioritization
16 condition, followed by the testing condition, then in the non-prioritization condition, and finally
17 in the absent in working memory condition. To contrast participant's accuracy across the
18 experimental conditions, we conducted a rm-ANOVA. Because the sphericity assumption was
19 violated ($\chi^2(42) = 21.42, p < .001, \epsilon = 0.75$), the Greenhouse–Geisser correction was applied.
20 Results suggested a main effect of condition, which was also supported by the very strong
21 evidence in favor of the alternative model as revealed by the Bayes factor: $F(3, 126) = 63.76,$
22 $p_{corr} < .001, \eta_p^2 = 0.60, BF_{10} = 6.36 \times 10^{21}$ (Figure 3a). The Bayes factor of the post-hoc tests
23 revealed very strong evidence for the accuracy difference between (i) the prioritization vs. non-
24 prioritization condition: $t(42) = 11.26, p_{adj} < .001, d_{av} = 0.75, 95\% \text{ CI } [9.76, 14.03], BF_{10 \text{ corr}} =$
25 1.057×10^{11} ; (ii) between the prioritization vs. absent in working memory condition: $t(42) =$

1 10.62, $p_{adj} < .001$, $d_{av} = 0.93$, 95% CI [12.18, 17.89], $BF_{10\ corr} = 1.806 \times 10^{10}$; (iii) between the
2 prioritization vs. testing condition: $t(42) = 10.52$, $p_{adj} < .001$, $d_{av} = 0.52$, 95% CI [6.61, 9.74],
3 $BF_{10\ corr} = 1.374 \times 10^{10}$; (iv) between the absent in working memory condition vs. testing
4 condition: $t(42) = -5.16$, $p_{adj} < .001$, $d_{av} = 0.40$, 95% CI [-9.54, -4.18], $BF_{10\ corr} = 1280.32$.
5 Additionally, strong evidence was found for the comparison between non-prioritization and
6 testing condition $t(42) = -4.18$, $p_{adj} < .001$, $d_{av} = 0.22$, 95% CI [-5.51, -1.92], $BF_{10\ corr} = 70.91$.
7 Finally, weak evidence was found for the contrast of non-prioritization vs. absent in working
8 memory condition: $t(42) = 2.44$, $p_{adj} = 0.01$, $d_{av} = 0.17$, 95% CI [0.54, 5.73], $BF_{01\ corr} = 0.96$.
9 Regarding our main hypothesis, the results suggest that both the prioritization and testing
10 condition resulted in higher accuracy compared to the absent in working memory condition
11 and non-prioritization condition. Interestingly, the testing condition still yielded benefits even
12 though participants did not report any locations in this case. Additionally, accuracy was higher
13 in the prioritization condition compared to the testing condition, indicating a greater long-term
14 memory boost for items undergoing attentional prioritization and testing compared to those
15 undergoing only testing in working memory. These findings remain consistent even when the
16 number of times an object appeared as a probe during the match-no-match task is controlled
17 (see Supplementary materials, section 2, Figure S2 for details).

18 ##### Table 2 #####

19 ##### Figure 3 #####

20 **2.6. Weak evidence for a response time decrease in the prioritizations vs. testing contrast**

21 **– evidence from Experiment 2**

22 As indicated in Table 2, at a descriptive level, participants were fastest in the prioritization
23 condition, followed by the testing condition, then in the non-prioritization condition, and finally
24 in the absent in working memory condition. We conducted an rm-ANOVA to investigate the
25 effect of condition on long-term memory response times. Sphericity was again violated

1 ($\chi^2(42) = 30.13, p < .001, \varepsilon = 0.65$), thus the Greenhouse–Geisser corrected results are reported:
2 $F(3, 126) = 9.94, p_{corr} < .001, \eta_p^2 = 0.19, BF_{10} = 2773.96$. The Bayes factor revealed again very
3 strong evidence for the alternative hypothesis, which predicts a main effect of condition (Figure
4 3b). The post-hoc tests revealed very strong evidence for the accuracy difference between the
5 prioritization vs. non-prioritization condition: $t(42) = -4.67, p_{adj} < .001, d_{av} = 0.36, 95\% \text{ CI } [-$
6 $160.97, -63.83], BF_{10\ corr} = 290.72$. Similarly, substantial evidence was found supporting the
7 difference between the (i) prioritization vs. absent in working memory condition: $t(42) = -3.47,$
8 $p_{adj} = .003, d_{av} = 0.37, 95\% \text{ CI } [-191.97, -50.83], BF_{10\ corr} = 10.42$ and (ii) the non-prioritization
9 vs. testing comparison: $t(42) = 3.10, p_{adj} = .006, d_{av} = 0.17, 95\% \text{ CI } [19.62, 92.83], BF_{10\ corr} =$
10 4.14 . Weak support was found for the prioritization vs. testing contrast, $t(42) = -2.94,$
11 $p_{adj} = .007, d_{av} = 0.19, 95\% \text{ CI } [-94.67, -17.67], BF_{10\ corr} = 2.86$. Finally, our analysis revealed
12 inconclusive evidence for the response times difference between the absent in working memory
13 condition vs. testing condition, $t(42) = 2.37, p_{adj} = .02, d_{av} = 0.19, 95\% \text{ CI } [9.70, 120.75], BF_{10}$
14 $corr = 0.83$ and substantial evidence for the lack of difference between the non-prioritization vs.
15 absent in working memory condition: $t(42) = -0.37, p_{adj} = .70, d_{av} = 0.02, 95\% \text{ CI } [-57.21,$
16 $39.22], BF_{01\ corr} = 0.07$. Overall, the results indicate that the prioritization condition was
17 associated with faster responses compared to the absent in working memory condition and non-
18 prioritization condition. For the testing condition, faster responses received substantial support
19 only when compared to the non-prioritization condition. The difference between the testing vs.
20 absent in working memory condition was only supported by the frequentist statistical
21 framework. Finally, weak evidence supported faster responses in the prioritization condition
22 compared to the testing condition. Overall, the response time results do not entirely mirror the
23 accuracy results; however, they suggest slightly decreased response times for information
24 undergoing attentional prioritization compared to testing in working memory.

1 **2.7. Enhanced parietal old-new component for prioritized and tested items in working**
2 **memory – evidence from Experiment 2**

3 Similar to Experiment 1, we investigated the parietal old-new effect as an EEG correlate of
4 long-term memory recollection. Data from the electrode cluster P1, P3, P5³⁴ were averaged
5 and contrasted across all six condition combinations using cluster-based permutation statistics.
6 The results revealed significant clusters between (i) 500-668 ms for prioritization vs. non-
7 prioritization, (ii) 232-696 ms for prioritization vs. absent in working memory condition, and
8 (iii) 432-612 ms for testing vs. absent in working memory condition (Figure 3c). The other
9 comparisons (prioritization vs. testing, non-prioritization vs. absent in working memory
10 condition, and non-prioritization vs. testing) were not statistically significant. These findings
11 suggest that long-term memory retrieval was enhanced both in the prioritization and in the
12 testing condition when compared to the absent in working memory condition. However, no
13 statistical support was found for the prioritization vs. testing contrast. When it comes to the
14 non-prioritization condition, we could replicate the result pattern from Experiment 1: we found
15 an enhanced parietal old-new effect for prioritization vs. non-prioritization, suggesting that the
16 benefit of attentional prioritization was beyond mere repetition. Additionally, the non-
17 prioritization vs. absent in working memory condition difference was again non-significant.
18 Finally, contrary to our expectation, the non-prioritization vs. testing contrast was not
19 significant, raising the question of whether at the neural level, these two conditions are
20 distinguishable.

21 **2.8. Comparable location decoding for prioritized and tested items in working memory –**
22 **evidence from Experiment 2**

23 Since our ERP analysis showed no differences between the prioritization and testing condition,
24 which contradicts the behavioral results, we aimed to further elucidate the neural mechanisms
25 underlying long-term memory retrieval of locations using a decoding procedure. Previous

1 research suggests that decoding approaches are suitable for tracking how certain information
2 is represented in the brain. Unlike univariate methods, multivariate methods can capture the
3 complex relationship between different input features (e.g., channels, frequencies)³⁵. We
4 wanted to investigate whether the location information stored in long-term memory underwent

5 ##### Figure 4 #####

6 any changes due to differential processing in working memory, with a specific focus on
7 tracking representational changes between the prioritization and testing condition.

8 As a first step in our analysis, we assessed whether we could decode the location
9 information in each experimental condition. Our classifier (support vector machine algorithm)
10 was trained to distinguish one retrieved location (e.g., left) from all other retrieved locations
11 (i.e., right, top, bottom) during the final retrieval phase. With four possible locations, the chance
12 level is 0.25. As shown in Figure 4a, we found significant above-chance decoding accuracy in
13 the: (i) prioritization condition (significant cluster: 520-836 ms); (ii) testing condition
14 (significant cluster: 88-1100 ms), and (iii) absent in working memory condition (significant
15 cluster: 1028-1200 ms). No statistically reliable effects were found in the non-prioritization
16 condition (Figure 4a). Since we could not successfully decode the location retrieval of the non-
17 prioritization objects, subsequent comparisons were conducted only for the three other
18 conditions.

19 In the second step, we compared decoding accuracy between these conditions. The
20 prioritization vs. absent in working memory condition comparison showed a significant cluster
21 between 472-640 ms, while the testing vs. absent in working memory condition contrast
22 showed a significant effect between 520-688 ms. No significant differences were found when
23 comparing the prioritization vs. testing condition (Figure 4b). These results align with the
24 parietal old-new pattern, indicating enhanced long-term memory representation for both the
25 prioritization and testing condition compared to the absent in working memory condition.

1

3. Discussion

2 In two experiments, we investigated whether attentional prioritization (Experiments 1 and 2)
3 and testing (Experiment 2) in working memory enhance long-term memory representations. A
4 unique aspect of this study was examining the impact of these working memory processes on
5 *existing* long-term memory representations that have been recently encoded but not yet
6 consolidated. Additionally, in contrast to previous studies investigating comparable processes
7 ^{21–23,25,26} we also explored these effects at a neural level. Behavioral and EEG results from
8 Experiment 1 demonstrated a clear long-term memory retrieval benefit from attentional
9 prioritization in working memory compared to the: (i) absence of information in working
10 memory and (ii) brief presentation and maintenance in working memory (non-prioritization
11 condition; also analogous to a repetition effect). Experiment 2 further revealed two important
12 patterns of results.

13 First, results of Experiment 2 suggested that both the combination of attentional
14 prioritization and testing (i.e., prioritization condition) and also testing in working memory
15 (i.e., testing condition) led to long-term memory benefits relative to a control condition, which
16 involved the absence of information in working memory. Importantly, in this context, the
17 testing effect was defined as the non-selective maintenance of information in working memory
18 to generate a response during the final match-no-match test. Moreover, in contrast to previous
19 studies, we provide evidence for a boost in long-term memory retrieval both at the behavioral
20 and at the neural level (ERP and decoding results). These findings add to previous literature
21 suggesting that different processes in working memory (i.e., elaboration, attentional
22 prioritization, testing) can lead to a differential built-up of information in long-term memory^{9–}
23 ^{15,17–26}. However, the present study offers a new perspective in this area, because it reveals that
24 even recently encoded, unconsolidated long-term memories benefit from processing in

1 working memory. Importantly, these benefits occur even when working memory processing is
2 implicit. Participants were instructed to treat the working memory phase separately from the
3 long-term memory task, and many were unaware that the objects appeared in the same locations
4 during the encoding phase and subsequent working memory phase (cf., answers in the follow-
5 up questionnaire). Thus, the observed enhancements in long-term memory retrieval are
6 unlikely to be attributed to consistent strategic efforts by participants to reinforce previously
7 encoded associations.

8 A key question in this context is understanding the mechanisms through which these
9 two conditions enhance long-term memory retrieval compared to the absent in working
10 memory condition. Several working memory processes likely contribute to this effect. First, in
11 the prioritization condition, the selective retro-cue leads to the prioritization and selective
12 maintenance of the cued item until the test. Consistent with previous research^{14,36}, the
13 presentation of the selective retro-cue enhances the object's representation and its report, which
14 in turn leads to the long-term memory retrieval benefit. In contrast, the testing condition did
15 not involve attentional prioritization but instead relied on the non-selective maintenance of
16 items until the working memory test.

17 Regarding the testing condition, we had two important observations. First, our results
18 suggest that even though the working memory test did not require a location report, but rather
19 a match no-match decision, this still benefitted long-term memory retrieval. This shows that
20 long-term memory retrieval can also be boosted via testing in working memory, even though
21 the working memory test and the final long-term memory test do not match. Second, results
22 reported in the Supplementary materials (section 1, Figure S1) suggest that objects in the testing
23 condition received a boost when presented as the central probe. Accordingly, items in the
24 testing condition that were never presented as probes resulted in significantly lower accuracy
25 compared to items that served as probes twice. Overall, this suggests that a non-specific

1 working memory test can strengthen long-term memory representations, likely due in part to
2 the additional boost items receive when serving as the central probe.

3 A second important finding of Experiment 2 is the dissociation between the behavioral
4 and neural patterns. Behavioral evidence suggested a robust increase in accuracy when both
5 attentional prioritization and testing were involved, compared to when only testing was
6 involved. A similar pattern was observed in response times, although the evidence was weaker.
7 At the neural level, a different pattern emerged. ERP results did not reveal a difference between
8 the prioritization and testing condition. However, when these two conditions were contrasted
9 with the absent in working memory condition (absence of information in working memory and
10 mere repetition of information in working memory), the prioritization condition differed from
11 both the absent in working memory condition, whereas the testing condition only differed from
12 the absent in working memory condition. Finally, decoding retrieved locations from the EEG
13 activity during the long-term memory task indicated no differences in the long-term memory
14 representation between the prioritization and testing condition.

15 These findings from Experiment 2 indicate that while attentional prioritization provided
16 a behavioral benefit over testing for long-term memory recall, this benefit was not mirrored at
17 the neural level. In our view, this discrepancy might be due to the short-lasting nature of the
18 neural benefits from attentional prioritization, which may not be detectable with EEG at the
19 scalp level. This suggests that other brain imaging techniques, such as fMRI or intracranial
20 EEG, may be needed to capture these subtle changes in neural activity.

21 Bringing together our findings, we argue that our results support the notion of
22 attentional prioritization and testing in working memory jointly enhancing the retrieval of long-
23 term memory content. This conclusion aligns with theoretical proposals from the working
24 memory literature that suggest a tight link between attentional prioritization and testing.
25 Accordingly, the prevailing view is that attentional prioritization in working memory always

1 serves a specific purpose, such as preparing for a final test or performing an action³⁷⁻³⁹.
2 Prioritizing and selecting information in working memory thus involves keeping the
3 information in a heightened state, protected from interference until it serves its purpose⁴⁰. Even
4 unprioritized information can be restored to a prioritized state, if the participant is aware that
5 this information is relevant for a subsequent test⁴¹. Consequently, information is only discarded
6 from working memory when participants are confident that it will not be needed later,
7 suggesting that attentional prioritization is driven by task-specific demands. Therefore, testing
8 in working memory provides a functional purpose for attentional prioritization, indicating that
9 these processes operate together to support effective memory retrieval and task performance.

10 At a broader level, our findings have significant implications for current theories of
11 long-term and working memory. Traditional views suggest that long-term memory retrieval is
12 mediated by working memory, which temporarily maintains retrieved long-term memory
13 content^{3,4,42}. Our results expand on these theories by indicating that working memory not only
14 serves as a temporary buffer, but it is an instance, where active processes, such as attentional
15 prioritization or testing can modify and strengthen the recently encoded long-term memory
16 representations. This suggests that the relationship between the two memory systems is far
17 more dynamic than previously thought, with working memory playing an active role in shaping
18 long-term memory representations that were recently encoded and are not yet fully
19 consolidated.

20 **Conclusions**

21 To summarize, our study provides novel insights into the interplay between working- and long-
22 term memory. Across two experiments, we collected data from 86 participants and
23 demonstrated that attentional prioritization and testing within working memory *jointly* enhance
24 the retrieval of existing long-term memory representations, with evidence at both behavioral
25 and neural levels. Our findings extend existing theoretical views by suggesting that working

1 memory does more than temporarily store retrieved long-term memory information; it can
2 actively strengthen it. By demonstrating that recently encoded, not yet fully consolidated long-
3 term memories benefit from working memory processes, our study highlights the critical role
4 of working memory in shaping durable long-term memory traces.

5 **4. Methods**

6 **4.1. Experiment 1**

7 **4.1.1. Participants**

8
9
10
11 Initially, data from 49 participants were collected, with six datasets excluded: four due to
12 technical issues with EEG recording and two due to misunderstandings of the task. One of the
13 latter participants consistently pressed the right button during the final retrieval phase, failing
14 to report any actual location. The second participant was excluded based on the verbal feedback
15 provided after the experiment, which revealed that the person misunderstood of the task. The
16 final sample comprised 43 participants (25 females, 18 males) aged 18 to 31 years ($M_{age} =$
17 23.65 years, $SD_{age} = 2.85$). We based our sample size on a previous investigation, in which we
18 investigated processes unfolding during long-term memory retrieval⁴⁵. All participants were
19 right-handed, had normal or corrected-to-normal vision, and reported no history of neurological
20 or psychiatric disorders. Compensation was provided either as a payment of 12 €/hour or as
21 study participation credits for psychology students. Written consent was obtained prior to
22 participation. The study was approved by the ethics committee of the Leibniz Research Centre
23 for Working Environment and Human Factors (Dortmund, Germany) in accordance with the
24 Declaration of Helsinki.

25 **4.1.2. Experimental procedure**

26 Upon arrival, participants were given an overview of the study and written consent was
27 obtained. Afterwards, they completed the German versions of a demographic survey and the

1 Edinburgh Handedness Inventory⁴³. Next, the EEG cap was prepared, and participants were
2 guided into the dimly lit EEG laboratory. The experiment was run on a 22-inch CRT monitor
3 (100 Hz; 1024×768 pixels) positioned at a viewing distance of ~145 cm. The experimental task
4 was programmed in Lazarus IDE (Free Pascal) and presented using the ViSaGe MKII Stimulus
5 Generator (Cambridge Research Systems, Rochester, UK). The procedure began with a short
6 training session, which was a short simulation of the main experiment.

7 The training consisted of 44 images (64 trials). This was followed by the main task,
8 which consisted of a combination of a long-term and working memory task with three phases:
9 an encoding phase, a working memory task, and a retrieval phase. Each phase was separated
10 by a five-minutes break. At the conclusion of the experiment, participants completed a follow-
11 up questionnaire, which asked about the strategies used by participants and encountered
12 difficulties. The session typically lasted between 3 and 4.5 hours.

13 **4.1.3. Stimuli and materials**

14 Stimuli for Experiment 1 were selected from a stimulus set comprising everyday objects⁴⁴.
15 Although the original pool included 260 objects, our selection was refined based on a prior
16 image rating survey⁴⁵, in which we selected a subset of 240 objects exhibiting optimal
17 luminance, contrast, vividness, and recognizability. Thus, for each participant, a random subset
18 of 180 images was selected for the task.

19 **4.1.4. Experimental paradigm**

20 During the encoding phase, participants viewed an everyday object (size: 253×177px or
21 177×253px, corresponding to 4.8°×3.35° or 3.35°×4.8° visual angle) on a gray background
22 (RGB 128-128-128) for 500 ms. The object appeared in one of four screen locations: top,
23 bottom, left, or right. Participants were instructed to memorize the object's location while
24 keeping their gaze fixed on a central black dot (size: 0.2°×0.2°), positioned ~3° from the

1 object's center (see Figure 1c). To aid memorization, they visualized the object in its location
2 after it disappeared, still focusing on the central dot, and were instructed not to use verbal
3 repetition or semantic information. At the end of each trial, participants confirmed
4 memorization by clicking the right button on the response device, initiating the next trial. Each
5 object was presented twice in the same location to facilitate learning, with all 180 objects shown
6 once before any were repeated.

7 The second phase of the task involved a working memory retro-cue paradigm.
8 Participants viewed a memory display for 300 ms, showing two objects from the encoding
9 phase (size: 253×177px or 177×253px, corresponding to 4.8°×3.35° or 3.35°×4.8° visual
10 angle) and two scrambled objects (size: 162×162px, corresponding to 3.07°×3.07° visual
11 angle) around a fixation dot (size: 0.2°×0.2°). The center of each object was ~3° from the
12 fixation dot. The two real objects appeared in their original encoding locations. The scrambled
13 objects were created using the GIMP software (<https://www.gimp.org/>) with the `fx_taqin`
14 command from the G'MIC plugin (<https://gmic.eu/>), resized to 162x162px before scrambling.
15 Participants were instructed to memorize the two real objects for a later report and ignore the
16 scrambled objects, which only acted as sensory fillers.

17 After a 500 ms maintenance period, a retro-cue (size: 1°×0.5° or 0.5°×1°) indicated
18 with 100% validity which item would be tested. The cue specified either the vertical or
19 horizontal axis. After an 800 ms interstimulus interval, participants saw a central probe object
20 and indicated whether it matched the cued object by pressing the top button for yes or the
21 bottom button for no, with response mapping counterbalanced across subjects. The central
22 probe matched the cued object 50% of the time (requiring a 'yes' response), it was a non-cued
23 object 25% of the time and a new object in 25% of the time. Overall, participants were supposed
24 to answer with a 'no' response in 50% of the trials.

1 Importantly, only 2/3 of the objects from the encoding phase were included in the
2 working memory task: one-third (60 objects) were consistently cued (prioritized), another one-
3 third (60 objects) appeared as non-cued / non-prioritized, and the remaining one-third appeared
4 only in the encoding and final retrieval phases (see Figure 1d). In each trial, a prioritized and a
5 non-prioritized object were randomly paired, ensuring one appeared on the horizontal axis and
6 the other on the vertical axis. Each object, bound to its location and condition, appeared four
7 times during this phase, resulting in 240 trials in total.

8 During the final retrieval phase, participants were shown all the objects from the
9 encoding phase (size: 253×177px or 177×253px, corresponding to 4.8°×3.35° or 3.35°×4.8°
10 visual angle). Their task was to report the location associated with each object during encoding.
11 They used a response device with four buttons mapped to the possible locations: top, bottom,
12 left, and right. Participants were instructed to keep their index finger on the middle of the device
13 between trials and return to this position after responding. To increase the number of trials,
14 each object's location was reported twice, resulting in a total of 360 trials (180 objects, each
15 presented twice).

16 **4.1.5. Data analyses**

17 MATLAB® (R2021b) was utilized for conducting all behavioral, EEG, and statistical analyses.
18 Initially, the dataset of each participant was segmented into three phases of the task: encoding
19 phase, working memory task, and retrieval phase. Since we were interested in the consequences
20 of differential processing in working memory, behavioral and EEG data from the retrieval
21 phase was analyzed.

22 **4.1.5.1. Statistical analyses**

23 We conducted our statistical analyses both using a frequentist and a Bayesian framework. The
24 former analyses were conducted using the functions of the Statistics and Machine Learning

1 Toolbox implemented in MATLAB® (R2021b). In case of the rm-ANOVA, Mauchly's test for
2 sphericity was applied. Whenever the sphericity assumption was violated, the Greenhouse–
3 Geisser correction (represented by ϵ) was employed. Partial eta squared (η^2) was calculated
4 as the measure of effect size. For the t-tests applied, unless otherwise noted, two-tailed p-values
5 were computed. Effect sizes were calculated using Cohen's d_{av} , following Lakens'
6 recommendations⁴⁶. For the post-hoc tests requiring multiple comparison adjustments, false
7 discovery rate⁴⁷ corrected p -values (denoted as p_{adj}) were provided .

8 The Bayesian statistical analyses were conducted in JASP (v.0.18.3)⁴⁸. Within the
9 Bayesian framework, Bayes factors denote the amount of evidence in favor of the alternative
10 or the null hypothesis. BF_{10} represents evidence in favor of an effect or condition difference,
11 while BF_{01} ($1/BF_{10}$) denotes evidence for the lack of an effect or condition difference. Bayes
12 factors lower than 3 have been interpreted as weak evidence, values between 3-20 as positive
13 or substantial evidence, Bayes factor ranging between 20-150 as strong evidence, and finally
14 values higher than 150 as very strong evidence⁴⁹. For both the rm-ANOVA and the Bayesian t-
15 tests, a multivariate Cauchy prior was adopted (as implemented in JASP). In case of the post-
16 hoc t-tests, corrected posterior odds are reported, which are denoted by $BF_{01\ corr}$ or $BF_{10\ corr}$.

17 **4.1.5.2. Behavioral analyses**

18 In order to answer our main research question, accuracy and response times recorded during
19 the retrieval phase were assessed. These two parameters were contrasted between the three
20 experimental conditions: (i) prioritization condition, which includes objects that were cued and
21 have undergone attentional prioritization in the working memory task; (ii) non-prioritization
22 condition, which includes objects that were present in the working memory task but did not
23 undergo attentional prioritization; (iii) absent in working memory condition, which includes
24 objects that were absent in the working memory task. Statistical comparisons were conducted

1 using a repeated measures analysis of variance (rm-ANOVA) with the within-subject factor
2 condition.

3 **4.1.5.3. Preprocessing**

4 The EEG data underwent preprocessing using the EEGLAB toolbox (version 14.1.2b; Delorme
5 & Makeig, 2004) implemented in MATLAB®. The first step of the preprocessing pipeline was
6 the application of a 0.1 Hz Hamming windowed sinc FIR high-pass filter (filter order: 33001,
7 transition bandwidth: 0.1 Hz, cutoff frequency at -6 dB: 0.05 Hz) and a 30 Hz low-pass filter
8 (filter order: 441, transition bandwidth: 7.5 Hz, cutoff frequency at -6 dB: 33.75 Hz) using the
9 `pop_eegfiltnew` function. Following this, channels exhibiting substantial noise were identified
10 and discarded through the automated channel rejection procedure in EEGLAB (for an
11 overview, see Table 1) (`pop_rejchan` function). As a next step, data were re-referenced to the
12 average. Notably, channels capturing anterior eye movements were excluded from rejection to
13 optimize eye-movement-related component detection in the subsequent independent
14 component analysis (ICA). Preparing for ICA, the data were downsampled to 200 Hz and
15 subjected to a 1 Hz Hamming windowed sinc FIR high-pass filter (`pop_eegfiltnew`, filter order:
16 661, transition bandwidth: 1 Hz, cutoff frequency at -6 dB: 0.5 Hz). Subsequently, epochs
17 spanning -1000 to 3000 ms relative to object onset were established, followed by baseline
18 correction (-200 to 0 ms). Trials exhibiting extreme fluctuations were then rejected via
19 EEGLAB's automated trial rejection procedure (for an overview, see Table 1) (`pop_autorej`;
20 threshold: 500 μ V, maximum % of rejected trials: 5%). Next, ICA was conducted on the rank-
21 reduced data (remaining number of channels minus one, determined via principal component
22 analysis within the `pop_runica` function). Identification of artifact-containing independent
23 components (ICs) was realized via the ICLabel plug-in (version 1.3; Pion-Tonachini et al.,
24 2019), which categorizes ICs into brain, muscle, eye, heart, line noise, channel noise, and other
25 noise. Following the criteria established by Wascher and colleagues (2022), ICs labeled with \geq

1 30% probability as eye movement components or < 30% probability as brain components were
2 discarded. Subsequently, the ICA weights were back-projected to the original 1000 Hz data,
3 followed by band-pass filtering and re-referencing. Data were again epoched (-1000 to 3000
4 ms) and underwent baseline correction (-200 to 0 ms). ICs marked for rejection were removed,
5 and trials with significant fluctuations were discarded using the same automated procedure
6 mentioned above (for an overview, see Table 1) (threshold: 1000 μ V, maximum % of rejected
7 trials: 5%). Finally, missing channels were interpolated using the spherical spline method in
8 EEGLAB (pop_interp).

9 ##### Table 3 #####

10 4.1.5.4. Event-related component analysis

11 In order to test our main hypothesis, we assessed the left parietal old-new ERP component,
12 previously argued to capture long-term memory recollection²⁸⁻³². First, data was downsampled
13 to 250 Hz. Next, we extracted the ERPs relative to the experimental conditions and data were
14 averaged across the left parietal electrode cluster (P1, P3, P5)³⁴. For the statistical comparison,
15 a cluster-based permutation procedure was adopted. This procedure was applied three times for
16 the (i) prioritization vs. non-prioritization condition; (ii) prioritization vs. absent in working
17 memory condition; and (iii) non-prioritization vs. absent in working memory condition
18 contrasts. For each analysis, the time window was restricted to 0-1200 ms after object onset.
19 The typical left-parietal old-new effect usually occurs between 500-800 ms^{32,34}; however, since
20 we adopted cluster-based permutation statistics, the time window was extended.

21 The first step of the cluster-based permutation procedure was to contrast the time series
22 of the two conditions using paired-sample t-tests. This resulted in a vector of 875 p -values,
23 each corresponding to a comparison from the original dataset. Clusters with more than one
24 significant p -value ($p < 0.05$) were identified based on this vector. In the next phase, a
25 distribution of maximum cluster sizes was created by randomly shuffling the condition labels

1 (e.g., prioritization and non-prioritization) within 1000 iterations. For each iteration, paired-
2 sample t-tests were performed at all time points to compare the voltage changes between each
3 condition. At each iteration, the largest cluster of significant p -values ($p < 0.05$) was recorded,
4 which resulted in a distribution of maximum cluster sizes. Finally, we determined the 95th
5 percentile of this distribution, and clusters exceeding this threshold were deemed significant.

6 **4.2. Experiment 2**

7 **4.2.1. Participants**

8
9 Data were initially collected from 45 participants, with two participants subsequently excluded.
10 One was removed for performing at chance level (25%) during the final retrieval phase, and
11 the other due to having mean reaction times that were six standard deviations away from the
12 group's average. The final dataset consisted of 43 individuals. The participants (25 females, 18
13 males) ranged in age from 20 to 34 years ($M_{age} = 24.97$ years, $SD_{age} = 3.94$). All other details
14 from Experiment 1 are also applicable to Experiment 2.

15 **4.2.2. Experimental procedure**

16 Experiment 2 included an experimental procedure identical to Experiment 1, with the only
17 difference that the training consisted of more trials and images (52 trials and 15 images) and it
18 was a simulation of the paradigm of Experiment 2.

19 **4.2.3. Stimuli and materials**

20 Since Experiment 2 contained a new condition, which required significantly more objects (i.e.,
21 300 in total), stimuli from the pool introduced by Brady and colleagues⁵³ was used. In total,
22 300 objects were manually selected.

23 **4.2.4. Experimental paradigm**

24 In Experiment 2, the encoding and retrieval phases were the same as in Experiment 1, but with
25 300 objects total, resulting in 600 trials for both phases. Due to using images from a different

1 dataset, both the target and scrambled objects were sized at 200 px×200 px (corresponding to
2 a visual angle of 3.8°×3.8°). A key difference from Experiment 1 was the introduction of a new
3 condition in the working memory task: a neutral cue (size: 1°×1°) condition (referred to as
4 testing condition) that provided no information about the to-be-tested item. Participants had to
5 determine whether any object from the original memory display matched the probe object.
6 Similar to Experiment 1, 50% of the probes were objects from the display, and 50% were
7 entirely new objects, never encountered in the task. In Experiment 2, objects were divided into
8 four conditions (see Figure 1d): (i) one-fifth were in the cued (prioritization) condition; (ii)
9 one-fifth were in the non-cued (non-prioritization) condition; (iii) two-fifths were in the testing
10 condition; and (iv) one-fifth were in the absent in working memory condition, not appearing in
11 the working memory task.

12 **4.2.5. Data analyses**

13 All aspects reported in case of Experiment 1 apply also for Experiment 2.

14 **4.2.5.1. Behavioral analyses**

15 In Experiment 2, we aimed to compare final long-term memory retrieval performance—
16 measured by accuracy and response times—across four experimental conditions using rm-
17 ANOVA. These conditions were: (i) prioritization condition, where objects were cued and
18 underwent attentional selection and testing in the working memory task; (ii) non-prioritization
19 condition, where objects were present in the working memory task but did not undergo
20 attentional selection or testing; (iii) absent in working memory condition, where objects were
21 absent from the working memory task; and (iv) testing condition, where objects were cued and
22 tested but did not undergo attentional selection (Figure 1d). Since Experiment 2 included more
23 objects and thus participants were required to learn more associations, we conducted a control

1 analysis to ensure that performance in Experiment 1 and 2 was comparable (see Supplementary
2 materials, section 3, Table S3).

3 **4.2.5.2. Preprocessing**

4 The preprocessing pipeline adopted for the ERP analysis of Experiment 2 was identical to the
5 pipeline adopted in case of Experiment 1. Nevertheless, in case of the decoding analysis, we
6 introduced some changes. First, except for a 1 Hz low-pass filter used to prepare data for the
7 ICA, filtering was entirely omitted, as prior research suggests that filtering might artificially
8 boost decoding results⁵⁴. Furthermore, because we wanted to maximize the number of trials
9 used for decoding, we opted to exclude the trial rejection procedure from this pipeline. As a
10 result, we had 120 trials per each condition (for the prioritization, non-prioritization, and
11 control condition), and 240 trials for the testing condition. With both filtering and trial rejection
12 omitted, we implemented channel rejection across the full range of electrodes.

13 ##### Table 4 #####

14 **4.2.5.3. Event-related potential analysis**

15 We applied the same analysis described in case of Experiment 1. Since Experiment 2 includes
16 four conditions, six different statistical comparisons were conducted, which enabled the
17 contrasting all conditions with all the other conditions.

18 **4.2.5.4. Decoding analyses**

19 Our analysis was centered on decoding the location retrieved during the final long-term
20 retrieval phase. First, we performed decoding within each condition and then compared the
21 decoding accuracy between conditions – except the non-prioritization condition, which did not
22 show above-chance decoding accuracy. Specifically, the classifier was trained to distinguish
23 between one vs. all the other retrieved locations (e.g., top location vs. all the other locations)
24 within each condition. Thus, the classification routine was run for each condition separately.

1 Following the methodology of Bae and Luck⁵⁵, we used a combination of support vector
2 machines and error-correcting output codes, implemented with the `fitcecoc()` MATLAB®
3 function, while testing and predictions were performed using the `predict()` function.

4 The decoding procedure's input consisted of power values from time-frequency
5 decomposition. We included twenty-six frequency bands between 4-30 Hz and 64 electrodes
6 as features. Classification was conducted separately for each participant and timepoint,
7 focusing on EEG oscillatory activity between -200 to 1300 ms. At each timepoint, trials for
8 each location were randomly divided into three groups, referred to as blocks. An equal number
9 of trials for each location were assigned to each block, and any extra trials were removed if the
10 total number could not be divided by three. Within each block, data were averaged for each
11 location label, resulting in three averages per location. We used trial averages instead of single
12 trial data, as previous investigations argued that averaging reduces noise⁵⁵. This also ensured
13 that results were not due to decoding object identity. Model training was performed on 2/3 of
14 these averages, with testing on the remaining 1/3 (i.e., 3-fold cross-validation). Each average
15 served once as the test dataset. Once all averages served as a test dataset, trials were reshuffled
16 and re-assigned to the blocks for averaging and this procedure was repeated for 10 iterations.
17 Predicted labels for all timepoints and iterations were compared to true labels to calculate
18 decoding accuracy. This was obtained and subsequently averaged across iterations. A five-point
19 moving time window smoothed these time series, and decoding accuracies were averaged
20 across participants. Since four locations were contrasted, the chance level was 25%.

21 First, we compared the decoding accuracy within each condition to chance level (0.25)
22 and next we compared it between conditions, using the cluster-corrected sign-permutation test
23 adopted by Wolff and colleagues⁵⁶. This method generates a null distribution by flipping value
24 signs with a 50% probability over 100 000 iterations (function: `cluster_test_helper`). Significant
25 clusters in the actual data were identified using this null distribution (function: `cluster_test`),

1 with significance thresholds set at $p < .05$. Based on the outcome of Experiment 1, we
2 hypothesized that the decoding accuracy should be greater than chance level and that the
3 decoding accuracy in the prioritization and testing condition should be higher than that in the
4 absent in working memory condition, one-tailed, cluster-corrected sign permutation tests were
5 used. Comparable to the ERP analysis, the statistical tests were limited to the 0-1200 ms
6 window.

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17 **Author contribution**

18 M.S.: data collection and data analysis. M.S. and D.S.: conceptualisation. M.S., L.I.K., D.S.:
19 writing the original draft. D.S.: project supervision and acquiring the necessary funding.

20 **Open practices and data availability statement**

21 The experiment was not preregistered. The raw data and all the scripts used for the reported
22 analyses will be publicly available after publication on Open Science Framework (OSF):
23 <https://osf.io/ne9yt/>

24 **Competing interest**

1 The authors declare no competing interests.

2

3

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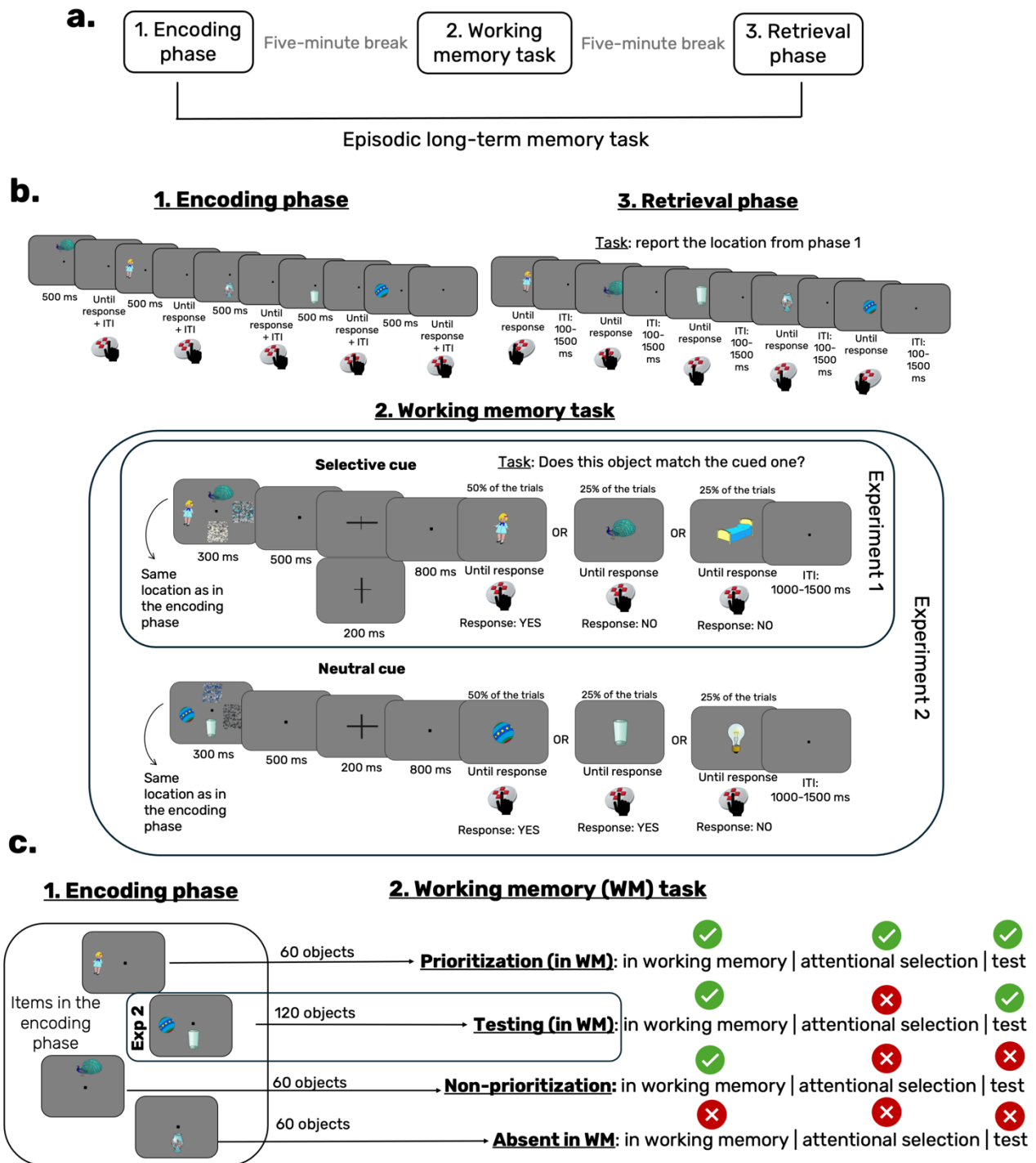
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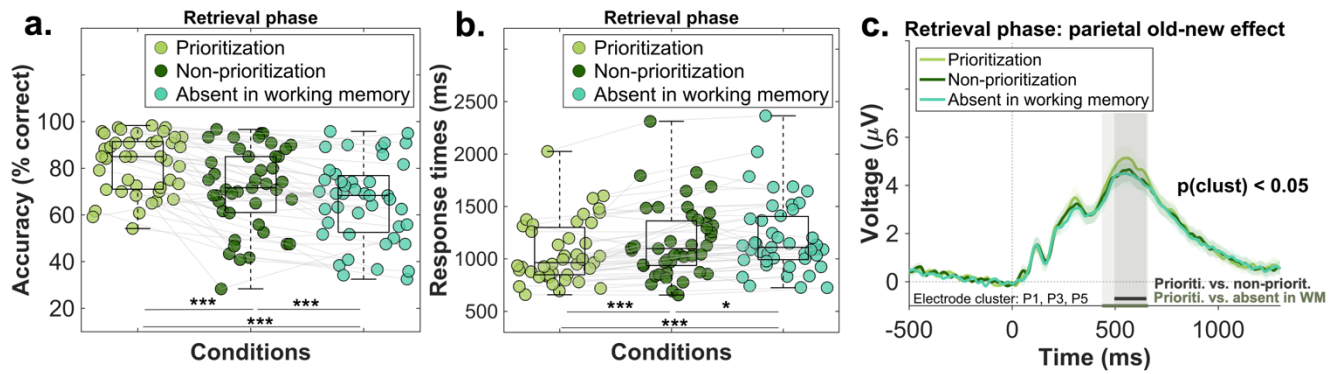
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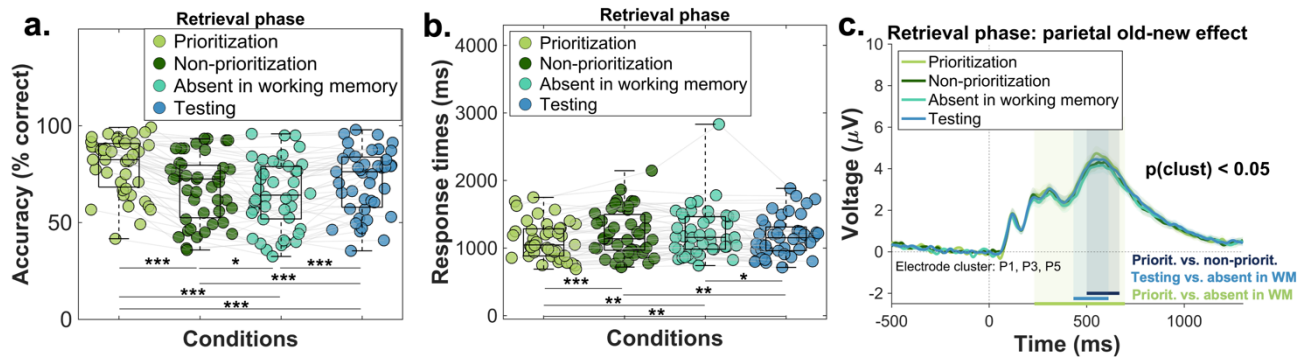
1 **Figure 1. Overview of the experimental design.** Panel a outlines the three main phases of the
 2 experiment, while Panel b offers a detailed breakdown of these phases. In Experiment 1, the working
 3 memory phase includes only selective (informative) retro-cues, whereas Experiment 2 incorporates both
 4 selective cues and neutral (non-informative) cues. Panel c demonstrates how the same objects from the
 5 encoding phase reappear during the working memory task, undergoing different types of processing
 6 depending on their assigned condition. For instance, in the "prioritization in WM" condition, the object
 7 undergoes both attentional selection and testing within working memory, while in the "absent in WM"
 8 condition, the object is not presented during the working memory task, appearing only during encoding

- 1 and the final retrieval phase. Notably, the "testing in WM" condition is exclusive to Experiment 2,
- 2 whereas the other three conditions are common to both experiments.
- 3



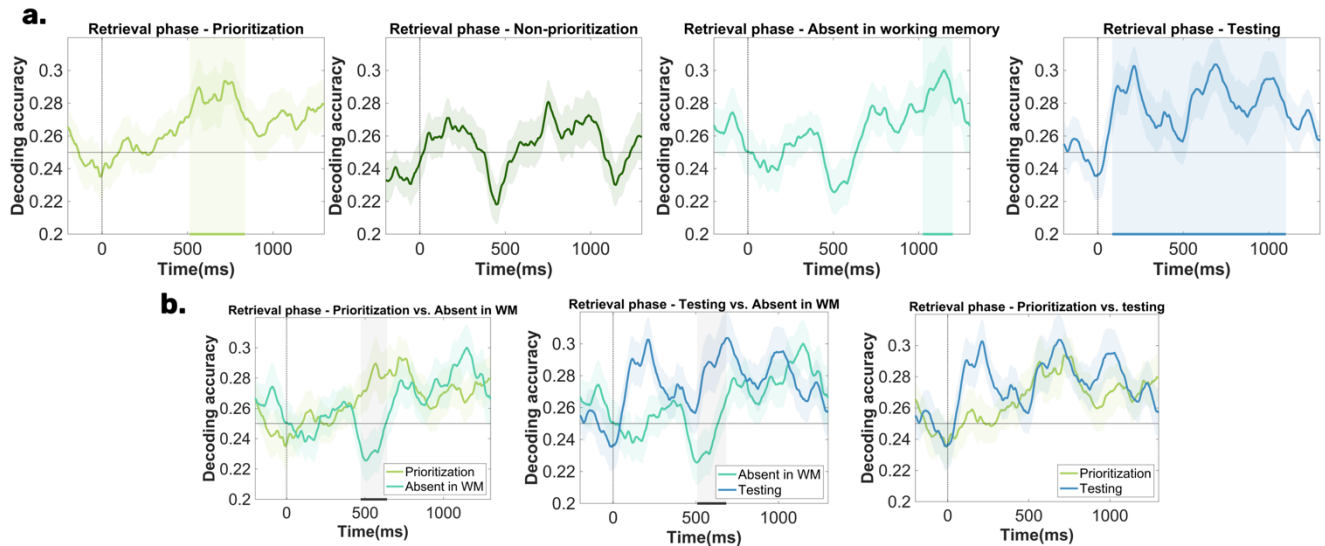
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2 **Figure 2. Results of Experiment 1.** The scatterplots of panel a and b illustrate the mean accuracy and
3 mean reaction time recorded during the three conditions of the final long-term memory retrieval phase.
4 The central mark in each boxplot represents the median, while the bottom and top edges denote the 25th
5 and 75th percentiles, respectively. The whiskers do not extend to averages, which are treated as outliers.
6 Grey lines connect data points from the same participant. Statistical significance is indicated with the
7 following symbols: * $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$. Panel c illustrates the parietal old-new effect
8 recorded during the same retrieval phase. The three shaded regions indicate the significant time window
9 identified through the cluster-based permutation analysis: (i) 496-652 ms for the prioritization vs. non-
10 prioritization contrast and (ii) 436-660 ms for the prioritization vs. absent in working memory
11 contrast. The shaded area around the ERP of each condition denotes the standard error of the mean.
12



1 **Figure 3. Behavioral and ERP results of Experiment 2.** The scatterplots of panel a and b illustrate
2 the mean accuracy and mean reaction time recorded during the four conditions of the final long-term
3 memory retrieval phase. The central mark in each boxplot represents the median, while the bottom and
4 top edges denote the 25th and 75th percentiles, respectively. The whiskers do not extend to averages,
5 which are treated as outliers. Grey lines connect data points from the same participant. Statistical
6 significance is indicated with the following symbols: * $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$. Panel c
7 illustrates the parietal old-new effect recorded during the same retrieval phase. The three shaded regions
8 indicate the significant time window identified through the cluster-based permutation analysis: (i) 500-
9 668 ms for prioritization vs. non-prioritization, (ii) 232-696 ms for prioritization vs. absent in working
10 memory condition, and (iii) 432-612 ms for testing vs. absent in working memory condition. The shaded
11 areas around the ERP of each condition denote the standard error of the mean.

12



1 **Figure 4. Decoding results during the final long-term memory retrieval phase.** The figure illustrates
2 the temporal evolution of average location decoding accuracy a. for the four experimental conditions
3 and b. for the condition contrasts. Panel a depicts the contrast between the decoding accuracy and
4 chance level (0.25). The green and blue shaded regions highlight the significant clusters: (i) 520-836
5 ms for the prioritization condition; (ii) 88-1100 ms for the testing condition; (iii) 1028-1200 ms for the
6 absent in working memory condition. Panel b shows the three conditions contrasts. The prioritization
7 vs. absent in working memory condition revealed a significant cluster between 472-640 ms and the
8 testing vs. absent in working memory condition contrast an effect between 520-688 ms, as indicated by
9 the grey shaded regions. The shaded area surrounding the decoding accuracy time series represents the
10 standard error of the mean.

11

1 **Table 1**

2 *Descriptive statistics – Experiment 1*

Mean and standard deviation (SD)

Condition	N	Mean accuracy	SD accuracy	Mean response times	SD response times
prioritization	43	81.68%	12.39%	1060.80 ms	294.63 ms
non-prioritization	43	71.12%	17.60%	1166.81 ms	342.96 ms
absent in working memory	43	65.91%	17.58%	1206.22 ms	350.33 ms

3

1 **Table 2**

2 *Descriptive statistics – Experiment 2*

Mean and standard deviation (SD) – Experiment 2

Condition	N	Mean accuracy	SD accuracy	Mean response times	SD response times
prioritization	43	79.65%	14.53%	1108.37 ms	273.99 ms
non-prioritization	43	67.75%	17.15%	1220.77 ms	342.00 ms
absent in working memory	43	64.61%	17.78%	1229.77 ms	369.52 ms
testing	43	71.47%	16.46%	1164.54 ms	291.11 ms

3

1 **Table 3**

2 *Overview of the outcome of each preprocessing pipeline*

Rejected number of channels	Number of remaining trials before ICA	Number of rejected IC components	Number of remaining trials after the ICA
$M = 1.62$ Range: 0-5	$M = 311.34$ (86.49 %) Range: 253-348 (70.27 % - 96.66 %)	$M = 31.97$ Range: 14-58	$M = 312.95$ (86.93 %) Range: 239-358 (66.38% - 99.44%)

3

1 **Table 4**

2 *Overview of the outcome of each preprocessing pipeline*

Analysis	Rejected number of channels	Number of remaining trials before ICA	Number of rejected IC components	Number of remaining trials after the ICA
ERP analyses	$M = 1.72$ Range: 0-5	$M = 491.46$ (82.02 %) Range: 363-559	$M = 32.46$ Range: 19-46	$M = 479.81$ (80 %) Range: 380-557
Decoding procedure	$M = 1.18$ Range: 0-5	$M = 500.60$ (83.51%) Range: 381-597	$M = 40.81$ Range: 26-50	-

3