

**THE ROLE OF WORKING MEMORY FOR MENTAL OPERATIONS  
ON LONG-TERM MEMORY**

by  
**DUYGU YÜCEL**

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**THE ROLE OF WORKING MEMORY FOR MENTAL OPERATIONS  
ON LONG-TERM MEMORY**

Approved by:

Asst. Prof. Eren Günseli .....  
(Thesis Supervisor)

Assoc. Prof. Çağla Aydın .....

Asst. Prof. Efe Soyman .....

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## ABSTRACT

### THE ROLE OF WORKING MEMORY FOR MENTAL OPERATIONS ON LONG-TERM MEMORY

DUYGU YÜCEL

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Thesis Supervisor: Asst. Prof. EREN GÜNSELİ

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mental operations

The role of working memory (WM) for information in long-term memory (LTM) has been debated over the years. While some studies suggest that WM is a buffer for LTM information, some indicate that LTM can bypass WM. By combining two different studies divided in two sections, this work aimed to reveal the role of working memory for mental operations on long-term memory. In the first section of this thesis, we examined the role of WM for information in LTM for mental integration and recognition. WM was found to be the standard buffer for LTM retrieval for mental integration but not for recognition. Thus, this study informed the interplay between WM and LTM for storing and processing information that humans require for most daily tasks. In the second section, we examined the effect of external attentional guidance on the interactions between WM and LTM with search and recognition tasks in a neuroimaging study. Although WM reactivation was present in all tasks, it was higher for recognition blocks. This finding suggests that participants continued to rely on WM to represent studied information if the information was stored for either a search or a recognition task, and attentional guidance demand has no effect on the interactions between WM and LTM. Overall, this thesis indicates that (1) the reactivation of spatial information in LTM is preserved mainly for mental integration task but not for recognition task, (2) the reactivation of object representations in LTM is not affected by attentional guidance demands. Further, our results support the idea that WM and LTM interactions are flexible and anticipatory.

## ÖZET

### UZUN SÜRELİ BELLEKTEKİ BİLGİLER ÜZERİNDEKİ ZİHİNSEL İŞLEMLER İÇİN İŞLEYEN BELLEĞİN ROLÜ

DUYGU YÜCEL

PSİKOLOJİ YÜKSEK LİSANS TEZİ, TEMMUZ 2023

Tez Danışmanı: Dr. Öğr. Üyesi EREN GÜNSELİ

Anahtar Kelimeler: çalışma belleği, uzun süreli bellek, dikkat, bellekte yeniden  
etkinleştirme, zihinsel işlemler

Uzun süreli bellekteki (USB) bilgi için çalışma belleğininin (ÇB) rolü yıllardır tartışılmaktadır. Bazı araştırmalar ÇB'nin USB'deki bilgiler için bir tampon bellek olduğunu öne sürerken, bazıları USB'nin ÇB'yi atlayabileceğini gösteriyor. Bu çalışma, iki farklı çalışmayı birleştirerek, zihinsel işlemler için ÇB'nin USB üzerindeki rolünü ortaya koymayı amaçlamıştır. İlk bölümde, zihinsel entegrasyon ve tanıma görevleri tamamlanırken USB'de bulunan bilgi için ÇB'nin rolünü inceledik. ÇB'nin zihinsel entegrasyon için USB için tampon bellek olduğunu, ancak tanıma görevi için olmadığı bulundu. İkinci bölümde, bir nörogörüntüleme çalışmasında dışsal dikkat rehberliğinin ÇB ve USB etkileşimi üzerindeki etkisini arama ve tanıma görevleri ile inceledik. ÇB'nin aktivasyonu tüm görevlerde olmasına rağmen, tanıma blokları için daha yüksekti. Bu bulgu, bilgilerin bir arama veya tanıma görevi için saklanması durumunda bilgileri temsil etmek için ÇB'ye güvenmeye devam ettiğimizi ve dikkatli rehberlik talebinin ÇB ve USB arasındaki etkileşimler üzerinde hiçbir etkisinin olmadığını göstermektedir. Genel olarak, bu tez, (1) USB'deki uzamsal bilginin yeniden etkinleştirilmesinin esas olarak zihinsel bütünleştirme görevi için korunduğunu ancak tanıma görevi için korunmadığını, (2) USB'de nesne temsillerinin yeniden etkinleştirilmesinin dikkat rehberliği taleplerinden etkilenmediğini gösterir. Dahası, farklı bilgi türleri ve görev talepleri için farklı yeniden etkinleştirme seviyeleri gözlemlediğimiz için, ÇB ve USB etkileşimlerinin esnek olduğu fikrini desteklemektedir.

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you lifted me. I'm grateful for everything you have done for me.

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*To the memory of my late father Yıldırım...*

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## 1. SECTION I

### 1.1 Introduction

Most daily tasks involve the effective functioning of working memory (WM), defined as the temporary storage, manipulation, and integration of information (Baddeley 1992; Baddeley and Hitch 1974; Logie 2003). The successful functioning of WM predicts higher-order cognitive skills, such as reasoning, problem-solving, and intelligence (Carpenter, Just, and Shell 1990; Chow and Conway 2015; Engle et al. 1999; Fukuda et al. 2010; Kane and Engle 2002; Süß et al. 2002). A common aspect of these skills is that they require mentally manipulating and integrating multiple pieces of information, such as when mentally trying out a chess move by taking separate piece arrangements into account. In line with this, these skills have been suggested to depend on mental manipulation and integration abilities of WM (Cho, Holyoak, and Cannon 2007; Christoff et al. 2001; Halford, Wilson, and Phillips 2010; Oberauer et al. 2008; Waltz et al. 1999).

Previous studies obtained behavioral and neural support for the importance of WM for performing mental operations. In dual-task paradigms, performing a WM task disrupted performance in a mental manipulation task (e.g., storage of colors vs. mental rotation (Hyun and Luck 2007); random number generation vs. mental addition (Logie, Gilhooly, and Wynn 1994). Moreover, fMRI studies found enhanced activity in regions associated with WM functioning during mental manipulation tasks (e.g., in the dorsolateral prefrontal cortex during mental rotation (D'Esposito et al. 1999; Glahn et al. 2002; Veltman, Rombouts, and Dolan 2003) despite successful cross-training across WM storage and mental operation tasks using fMRI and

EEG. Together, these studies suggest that mental operations require higher WM processing than mere storage even though information stored for mental operations is qualitatively no different from the information that is merely stored.

However, these studies provided novel information to participants on each trial, inherently necessitating WM involvement (Hyun and Luck 2007; D’Esposito et al. 1999; Glahn et al. 2002; Veltman, Rombouts, and Dolan 2003). Yet, humans often need to use existing information for mental operations, such as when mentally trying out a chess move based on an arrangement that was encoded a while ago (Baddeley 2002; Vandierendonck, Dierckx, and Van der Beken 2006). Thus, exploring the mechanisms of mental operations on existing long-term memories is crucial for forming a broader and ecologically valid understanding of memory and its role in mental operations.

Accordingly, here we assessed the importance of WM for integrating previously learned information available in long-term memory (LTM). In the study phase, participants learned color-position associations (Figure 1a). In the experimental session, they were given a color retrieval cue (Figure 1b). The position associated with this cue was either used in recognition or a mental operation task. The mental operation task was in the form of mental integration, where participants computed the position equidistant to two memory positions. There was also a perceptual discrimination task embedded within these main tasks that took place following the retrieval cue before the main task probe. We assessed the involvement of spatial WM using the well-established relationships between WM and perception. Specifically, previous studies observed enhanced perceptual discrimination at positions stored in WM (Awh and Jonides 1998, 2001; Awh, Jonides, and Reuter-Lorenz 1998; Awh, Vogel, and Oh 2006; Downing 2000). Thus, facilitated perceptual discrimination at LTM vs. irrelevant positions can be interpreted as reactivation of LTM positions on WM.

Emphasizing the importance of working memory for mental operations, we hypothesized that reactivation of LTM positions should result in facilitated perceptual discrimination at LTM vs. irrelevant positions for mental integration condition (Fukuda and Woodman 2017; Vo et al. 2021). On the other hand, the lack of LTM position benefit in recognition condition would support the studies suggesting that recognition tasks can be performed using passive LTM (Carlisle et al. 2011; Gunseli, Meeter, and Olivers 2014; Gunseli, Olivers, and Meeter 2014). This outcome would be in line with theories of learning and automaticity that postulates repeatedly used information require little cognitive resources (Logan 1988; Logan and Gordon 2001; Shiffrin and Schneider 1977) and a recent paper that suggests LTM retrieval can bypass reactivation in WM (Liu et al. 2022).

To sum up, by using a behavioral marker of spatial WM following an LTM retrieval cue, we compared the role of WM in storing information available in LTM for recognition and mental integration tasks. Results have shown that our cognitive mechanisms prefer to reactivate LTM in WM for mental integration, but not for recognition. Our results contributed to the knowledge regarding the interplays between WM and LTM by revealing the aspects of this interplay regarding mental operations, thus informing our understanding of how memory systems interact to guide our behaviors.

## 1.2 Method

### 1.2.1 Participants

Students of Sabanci University between the ages of 18 and 35 participated for the course credit. All participants (15 women; 6 men) reported having a normal or corrected-to-normal vision and no color blindness. Participants who performed with an average accuracy or reaction time (RT) more than 2.5 standard deviations above or below the mean for either the main task or the perceptual discrimination task in recognition and mental integration condition were excluded from analyses. This study was conducted in accordance with the Declaration of Helsinki and is already approved by the Sabanci University's Research Ethics Council (SUREC). Informed consent was given prior to the experiment.

### 1.2.2 Stimuli

To compare the level of WM activation for representing information available in LTM, the proposed experiment employed a perceptual discrimination task embedded in the recognition and mental integration conditions. Given that previous studies showed higher perceptual discrimination at positions held in WM, we hypothesized that perceptual discrimination performance will be better at LTM positions relative to other, non-memory positions if the spatial information available in LTM is reactivated in WM.

The stimuli set was generated using PsychoPy3 v.2020.2.0 (Peirce et al. 2019). The data was collected online using Pavlovia. The experiment took 75-80 minutes. The experiment consisted of three phases: study, test, and experimental. At the

beginning of the experiment, the experimenter familiarized participants with the experiment by providing instructions with screenshots that demonstrated the experimental procedure for all the phases. All stimuli were presented on a computer screen. In the study and test phases, participants learned color-position associations (Figure 1.1). The background color was grey (RGB = 128, 128, 128). Each memory position was shown on one of eight black placeholders (RGB = 0, 0, 0;  $1.8^\circ$  of radius) placed equidistantly on a reference circle ( $21.58^\circ$  of radius) centered at fixation. The memory positions were paired with color retrieval cues ( $.72^\circ$  of radius). The following eight colors were selected as retrieval cues to achieve maximum discriminability: red (RGB = 255, 0, 0), orange (RGB = 255, 165, 0), purple (RGB = 128, 0, 128), blue (RGB = 0, 0, 255), turquoise (RGB = 64, 224, 208), green (RGB = 0, 128, 0), lime (RGB = 0, 255, 0), and yellow (RGB = 255, 255, 0).

### 1.2.3 Procedure

Figure 1.1 demonstrates an example of experimental procedure. The learning phase started with the presentation of retrieval cues and their associated positions. All eight retrieval cues and their associated positions were presented, first in a fixed order in a clockwise direction, then three times in a shuffled order. For each presentation, the retrieval cue was presented at the centre of the screen for 4,000 ms, and after a blank interval of 2,000 ms, the cued circle appeared at its associated position for 2,000 ms. Participants were instructed to associate retrieval cues that appear at the centre and their related position on the reference circle. After the learning session, participants proceeded to the test session. At the beginning of each test trial, a retrieval cue was shown. Participants were instructed to bring the associated position to their minds. Participants were expected to click on the correct position associated with the retrieval cue on the reference circle using the mouse. Participants were given feedback regarding their accuracy. After an inaccurate answer, participants were shown the correct memory position for 2000 ms and were redirected to the study session. To proceed to the experimental session, participants needed to correctly answer 16 times in a row (i.e., two times for each color-position association). The test phase was repeated until this threshold was achieved.

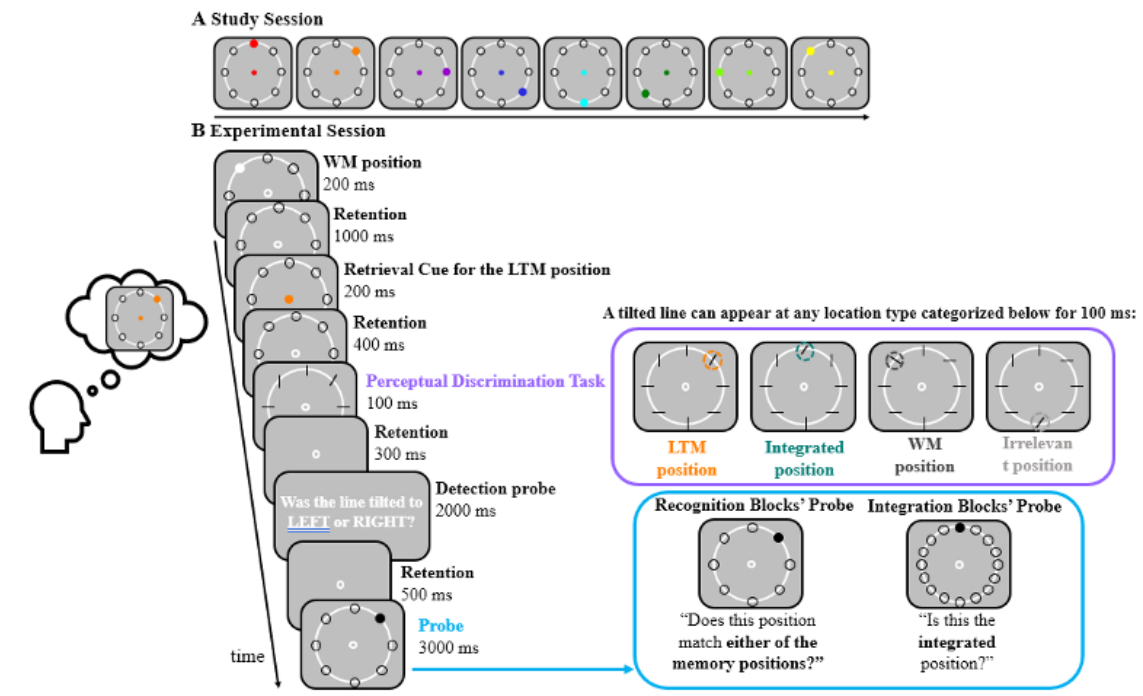
The experimental session consisted of two main conditions (recognition, and mental integration; Figure 1.2). These conditions were blocked. Within both conditions, a perceptual discrimination task was embedded as a secondary task. Participants initiated each trial by pressing the spacebar. Each trial began with the presentation of the fixation circle ( $.72^\circ$  of radius) for 300 ms. Then, the working memory display

was presented for 200 ms, which consisted of a white circle (RGB = 255, 255, 255; 1.8° radius) in one of the eight black placeholders. After a blank retention of 1000 ms, the retrieval cue (.72° of radius) was shown for 200 ms. Here, participants were recommended to bring the cued position in their mind's eye when the retrieval cue is presented. After another blank of 400 ms, eight black lines (one tilted target line and seven horizontal or vertical distractors; .1° line thickness; RGB = 0, 0, 0) were shown for 100 ms. The positions of the lines overlapped with the placeholders, hence with all possible memory positions. The target was tilted to the right or left by 35 or 55 degrees. After a retention of 300 ms, participants were asked to report if the target line was tilted to the left or right by pressing the “A” or “S” keys, respectively. Participants had a total of 2000 ms to respond to the perceptual discrimination task from the onset of the perceptual discrimination display. They were instructed to aim for speed without risking accuracy. After a blank interval of 500 ms, the probe display for the main task (recognition or mental integration) was presented until response or up to 3000 ms.

The probe display contained a black circle for both conditions. In the recognition condition, participants were instructed to respond to whether the black circle was in the same position as one of the memory positions by pressing “K” for match and “L” for no-match. In the mental integration condition, participants were asked to indicate if the black probe circle matches the integrated position(s) by pressing “K” or is different from the integrated position(s) by pressing “L.” The integrated position was defined as the circle equidistant to the two memory positions on the shorter arc of the reference circle. Before starting the experiment, we explained to participants how to integrate the two positions; by computing the point equidistant to the two memory positions on the shorter arc of the reference circle, not on the longer arc (a position that connects WM and LTM from the far side).

When the degree difference between WM and LTM is 180 degrees, there were two correct integrated positions on each side of the reference circle, as there is no shorter arc by definition. Therefore, we excluded such trials from the analysis. The probe in the mental integration condition appeared in any of 16 placeholders that consist of 8 placeholders for possible memory positions as in the recognition condition and 8 additional in-between placeholders between 8 constant memory positions. After the response, feedback was provided on the accuracy of both tasks. In the recognition condition, the feedback screen displayed at the end of each trial included the presentation of the previously shown white working memory circle and the cued long-term memory circle. In the mental integration condition, the feedback screen also included the correct integrated position in dark grey (RGB = 64, 64, 64).

Figure 1.1 The experimental procedure



(a) The time course of events in the study session. (b) The time course of events in the experimental session

### 1.2.4 Trial Distributions & Block Design

The experimental design was a 2 x 4 factorial, with two within-subject factors: x 2 conditions (recognition, mental integration) and x 4 target positions for the perceptual discrimination task (LTM, WM, integrated, irrelevant). The integrated positions were defined as all positions between WM and LTM on the shorter arc of the reference circle. The target line appeared at the WM and LTM positions in 14% of the trials, at the integrated position in 11% of the trials, and at irrelevant positions in 12% s. The position of the target line in the perceptual discrimination task was equally likely to be placed on each placeholder, with its order randomly intermixed across trials. For each participant, there were 32 memory-match trials for both memory positions (WM and LTM). In some trials, WM and LTM appeared on the exact opposite sides of each other in the mental integration condition. For these trials, we instructed individuals to perform the integration on either side and that either equidistant position will be accepted as the correct integrated position. However, given that we cannot know which side they performed integration, we excluded these trials from the analyses. Moreover, to match the trial types across

conditions, such trials were also excluded from the recognition task analyses.

There were 4 sequential blocks of either the mental integration or recognition condition, making a total of 224 experimental trials per condition. The order of the conditions was counterbalanced across participants. At the end of each block, participants received feedback on their block average accuracy and were encouraged to take a short break. For each participant, there were 32 trials for each combination of conditions (recognition, integration) and positions (working memory, long-term memory). Before each condition, there was a practice session to familiarize participants with that particular condition. The experimental procedure of practice trials was identical to the experimental trials except for the following. The presentation time of the tilted target line was 150 ms. Participants had 3000 ms to respond during the perceptual discrimination task probe and 5000 ms during the memory probe. The practice session contained 16 trials. To complete the practice session, participants needed to respond correctly on at least 10 trials for the main tasks and at least 4 trials for the perceptual discrimination task. The practice session was repeated until this threshold was reached. Participants who could not achieve this threshold in five attempts were not allowed to continue to the experimental session.

## 1.3 Results

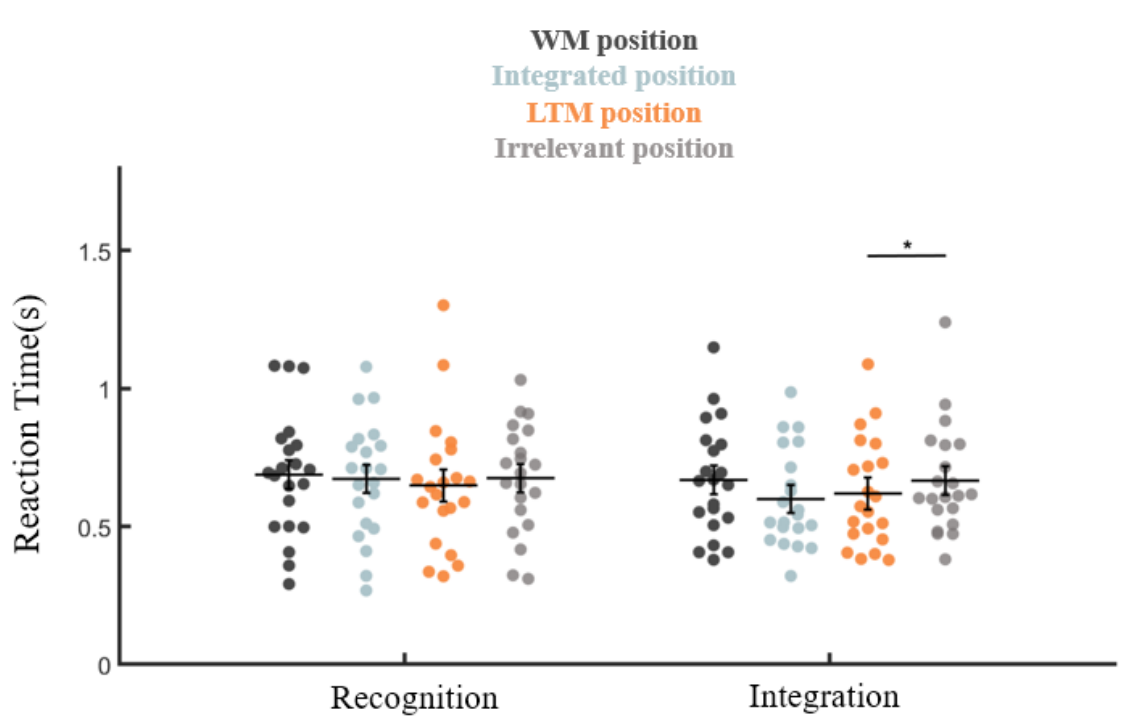
The target line in the perceptual discrimination task can appear on each of eight possible memory positions, thus resulting in four possible conditions regarding its overlap with the main-condition-related positions: WM position, LTM position, integrated positions, and irrelevant positions. For analysis purposes, the integrated position was defined as all positions in-between the WM and LTM positions to account for attention spreading across these positions in the mental integration condition on the short arc.

### 1.3.1 Line Detection Task Results

Average accuracy for the line detection task did not significantly differ between recognition ( $M = 0.76$ ,  $SD = 0.16$ ) and mental integration conditions ( $M = 0.76$ ,  $SD = 0.15$ ) ( $d = 0.045$ ,  $BF_{10} = 0.232$ , 95% HPD = [-0.358, 0.440],  $t(20) = 0.207$ ,  $p = 0.838$ ). Similarly, RT did not show a significant difference between conditions (MRecognition = 0.67, SDRecognition = 0.20; MIntegration = 0.65, SDIntegration

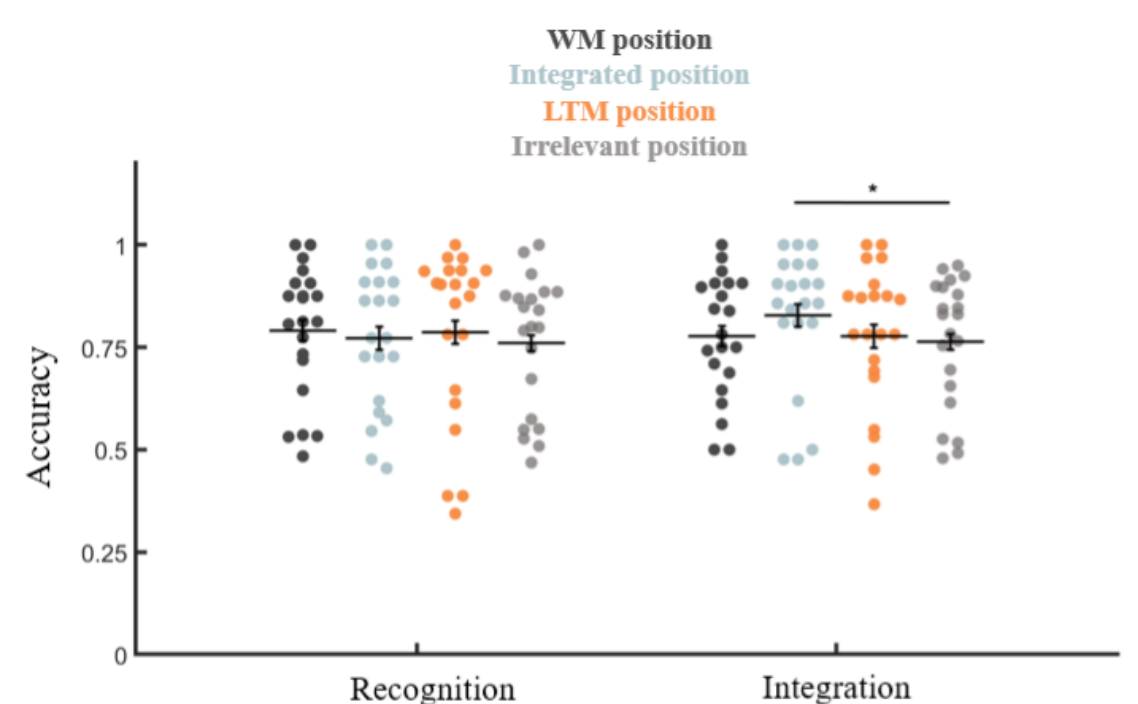
= 0.19) ( $d = 0.088$ ,  $BF_{10} = 0.245$ , 95% HPD = [-0.321, 0.479],  $t(20) = 0.403$ ,  $p = 0.691$ ). Figure 2.2 and Figure 2.3 shows the average accuracy and RT in the perceptual discrimination task for different position types (WM, Integrated, LTM, and Irrelevant). Participants ( $N = 21$ ) were faster to discriminate the lines appearing at the LTM position compared to the irrelevant positions in the mental integration condition ( $d = 0.58$ ,  $BF_{10} = 3.582$ , 95% HPD = [0.078, 0.977],  $t(20) = 2.657$ ,  $p = 0.015$ ), but not in the recognition condition ( $d = 0.18$ ,  $BF_{10} = 0.313$ , 95% HPD = [-0.239, 0.570],  $t(20) = 0.843$ ,  $p = 0.409$ ). The difference in LTM position benefit between the conditions did not reach significance ( $d = 0.230$ ,  $BF_{10} = 0.371$ , 95% HPD = [-0.201, 0.614],  $t(20) = 1.052$ ,  $p = 0.305$ ). There was no significant accuracy difference between LTM and irrelevant positions in the mental integration condition ( $d = 0.168$ ,  $BF_{10} = 0.293$ , 95% HPD = [-0.551, 0.256],  $t(20) = 0.789$ ,  $p = 0.439$ ) nor the recognition condition ( $d = 0.210$ ,  $BF_{10} = 0.343$ , 95% HPD = [-0.217, 0.595],  $t(20) = 0.962$ ,  $p = 0.343$ ). Thus, the RT results cannot be attributed to a speed-accuracy trade-off. In addition, participants were faster at responding when the tilted line appeared at the integrated position compared to irrelevant positions in the mental integration condition ( $d = 0.715$ ,  $BF_{10} = 11.48$ , 95% HPD = [0.181, 1.126],  $t(20) = 3.276$ ,  $p = 0.004$ ), and not in the recognition condition ( $d = 0.04$ ,  $BF_{10} = 0.233$ , 95% HPD = [-0.355, 0.443],  $t(20) = 0.22$ ,  $p = 0.825$ ). This finding may reflect the initiation or completion of mental integration at the time of the perceptual discrimination task onset on some trials.

Figure 1.2 Perceptual discrimination reaction time results



Mean reaction time (RT) given separately for each block type and position in the perceptual discrimination task. Error bars show the standard error of the mean calculated for the RT difference between working memory, long-term memory, integrated, and irrelevant position conditions.

Figure 1.3 Perceptual discrimination task accuracy results

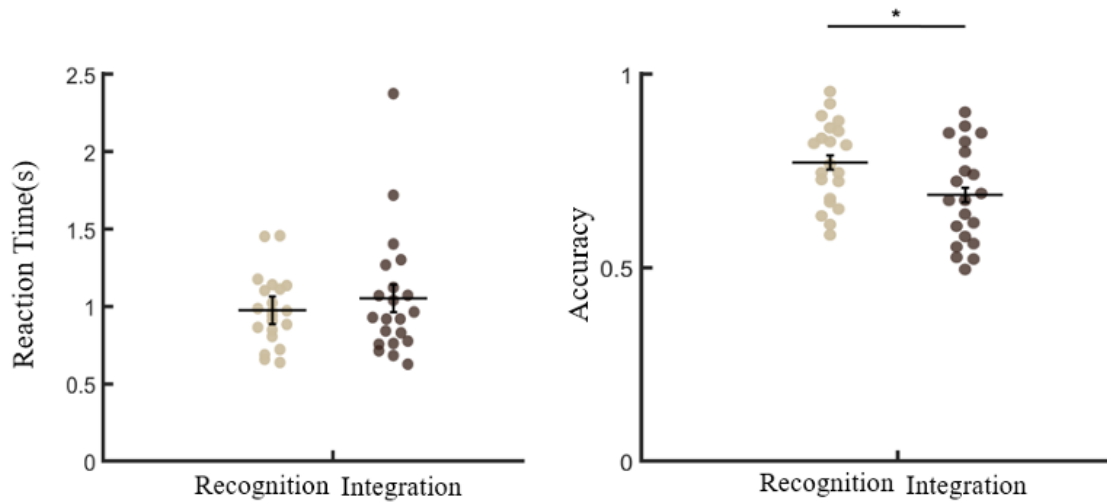


Perceptual discrimination accuracy for all of the position types across two different conditions.

### 1.3.2 Main Task Results

Figure 2.7 shows the average RTs and accuracy for the main tasks. Mean accuracy was higher for the recognition condition ( $M = 0.77$ ,  $SD = 0.11$ ) compared to the mental integration condition ( $M = 0.69$ ,  $SD = 0.14$ ) ( $d = 0.99$ ,  $BF_{10} = 151$ , 95% HPD = [0.393, 1.443],  $t(20) = 4.544$ ,  $p = 0.0002$ ). There was no RT difference between main task conditions ( $M_{\text{Recognition}} = 0.98$ ,  $SD_{\text{Recognition}} = 0.224$ ;  $M_{\text{Integration}} = 1.056$ ,  $SD_{\text{Integration}} = 0.448$ ) ( $d = 0.174$ ,  $BF_{10} = 0.302$ , 95% HPD = [-0.248, 0.560],  $t(20) = 0.796$ ,  $p = 0.435$ ).

Figure 1.4 Main task accuracy and reaction time results



Mean accuracy for the main tasks is shown separately for recognition and mental integration conditions.

## 1.4 Discussion

This study aimed to investigate the flexible interactions between WM and LTM for mental operations (mental integration and recognition). Adapting the methodology of earlier research showing that perceptual discrimination performance enhances positions in WM (Awh, Jonides, and Reuter-Lorenz 1998; Awh, Vogel, and Oh 2006; Awh and Jonides 1998, 2001; Downing 2000), we embedded a perceptual discrimination task before the main tasks as a proxy for the reactivation of LTM in WM. We were able to measure the reactivation of LTM in WM with a perceptual discrimination task, and future studies can use this method to measure WM and LTM interactions.

Supporting the previous studies which have shown the importance of WM for mental operations (D'Esposito et al. 1999; Glahn et al. 2002; Hyun and Luck 2007; Logie, Gilhooly, and Wynn 1994; Veltman, Rombouts, and Dolan 2003), the findings of this study suggest that WM is crucial for mental operations performed with novel information and information stored in LTM. In reflection on daily life, when we integrate novel information with previously learned information available in LTM, the information is represented in WM. Although findings emphasize the importance of WM for integration, it might mean that information stored in LTM is vulnerable

to distractors when used for mental operations. A past study showed that LTM is more resilient to perceptual distractors than WM (Blalock 2013). Representing information in WM is susceptible to interference, and distractors cause memory errors (Hallenbeck et al. 2021). Based on the findings, it might be a better strategy for people to integrate information in an environment that does not contain distractors to preserve the initial representation of the studied information.

On the other hand, our results revealed that our cognitive mechanisms do not prefer to reactivate LTM in WM for recognition tasks, meaning that information in WM and LTM is represented separately when we simply try to identify information. While results for recognition task supports the previous studies suggesting that recognition tasks can be performed with passive LTM representations (Carlisle et al. 2011; Gunseli, Meeter, and Olivers 2014; Gunseli, Olivers, and Meeter 2014) and constantly used information takes little cognitive effort due to automatization of the process by time (Logan 1988; G. D. Logan and Gordon 2001; Shiffrin and Schneider 1977), it contradicts the studies that perceive WM as a buffer for LTM operations (Fukuda and Woodman 2017). Although the LTM advantage for mental integration condition is significant, its interactions with the recognition conditions did not reach significance in our online study with 21 participants. A larger LTM position advantage for perceptual discrimination performance in the mental integration vs. recognition condition could support the view that WM is particularly important for mental operations (D’Esposito et al. 1999; Glahn et al. 2002; Logie, Gilhooly, and Wynn 1994; Veltman, Rombouts, and Dolan 2003). This outcome would have suggested that WM reactivation is preserved mainly for particular task demands, supporting the strategic involvement of WM to store information (Mızrak and Oberauer 2022). However, our results did not provide support for those studies. One explanation for the lack of significance in the interaction might be the number of participants who attended the study.

Although our perceptual discrimination task is a valid proxy for measuring the reactivation of LTM in WM, the study has some limitations. First, results show that participants can understand the instructions and perform the tasks. However, it contains weak evidence for interactions between the two conditions, as the LTM position benefit was only present in the mental integration condition. However, the lower main task accuracy in the mental integration condition suggests that it might be more difficult than the recognition task. This suggests that the LTM position benefit in the mental integration condition may be related to the difficulty instead of the mental operation characteristics of the task. A harder mental integration task might result in better connectivity between neural networks. To eliminate this possibility, a further study might replicate this study with a harder recognition task

or a simpler mental integration task such that the behavioral performance will be equated across two tasks. Second, participants might reactivate LTM in WM representations not more but earlier for mental integration task since they need to complete the mental integration before the probe appears. To test this, a future study can manipulate the stimulus onset asynchrony between the retrieval cue and the line detection task. In addition, one might criticize that we did not observe faster detection performance for WM information presented at the beginning of each trial in the form of the white circle. We suggest that this is due to the WM position being presented first. Previous studies in WM have shown that more recently presented information is kept at the focus of attention (Meiran, Cole, and Braver 2012; Oberauer 2001, 2002), while older, or less relevant information lies on the outside of the focus. Thus, it is possible that the more recently presented retrieval cue meant that information retrieved from LTM was in the focus of attention.

In summary, by using a behavioral index first time in the literature, we have shown that LTM information is reactivated in WM for mental integration task, but not for recognition task. Due to the vulnerable nature of WM towards attention, integrating information from LTM and WM in a distraction-free environment can help preserve the LTM information. Further, future studies can adapt perceptual discrimination task in the experiments to assess LTM reactivation in WM behaviorally.

## 2. SECTION II

### 2.1 Introduction

We rely on the internal representation of objects to perform a successful search. For example, when we search for our favorite snack in the supermarket, we have an activate template including the representation of the item. These representations, thy name active templates, are stored in visual working memory (VWM; Bundesen 1990; Bundesen et al. 2005; Desimone and Duncan, 1995). WM representations are proposed as a guide of attention, such that they direct attention to items that match memory representations (Desimone and Duncan, 1995; Gunseli et al., 2016; Olivers et al. 2006). Although previous studies were interested in the guide of attention during visual search tasks, in the typical setup, these studies used novel information for the tasks. In daily life, as in the supermarket example, we often search for information already stored in long-term memory (LTM). In this study, we aim to investigate the interaction between WM & LTM for anticipation of guiding external attention when previously learned targets available in LTM are re-experienced.

Attentional guidance demands increase with search requirements. Previous studies have shown that attentional templates in search tasks require stronger internal attention than recognition tasks (Gunseli et al. 2014; Gunseli et al. 2014; van Driel et al. 2017). In line with previous findings, these results are indications of the close relationship between WM and attention (Awh, Vogel, and Oh 2006; Awh and Jonides 2001; Downing 2000). Consistent with this, WM can be a mental workspace for information stored in LTM when external attentional demand is present. The guidance of WM results in faster reaction times in search displays and movement of

saccades to the same place with the information preserved in WM (Soto et al. 2005; Soto, Humphreys, and Heinke 2006). While WM seems to be in control when we face constant change in the environment, as a result of perceiving the same search targets, attentional templates are shifted back to LTM from WM. The decline in contralateral delay activity (CDA), which is an index of WM activation, was observed with the repetition of the same target across the experiments (Carlisle et al. 2011; Gunseli et al. 2014; Gunseli et al. 2014; Reinhart and Woodman, 2014). Likewise, search RTs decrease across a few repetitions of the same target across trials, paired with a reduction in the EEG and behavioral indices of WM storage. These improvements in visual search performance as attentional templates shift from WM to LTM are in line with theories of learning and automaticity and suggest that operating on ‘autopilot’ can result in better performance (Anderson 2000; Anderson 2009; Bocanegra and Hommel 2014; Logan 1979, 1988, 2002; Poldrack and Gabrieli 2001; Schneider and Shiffrin 1977; Woodman and Luck 2007). Overall, these findings suggest that WM and LTM can both guide attention, and in some cases, it is more effective to guide attention directly from LTM for existing information in LTM.

To test the possible flexible anticipatory interactions between WM and LTM in the preparation of external attentional guidance, we used CDA since it is a well-known EEG index of WM storage (Gunseli et al. 2018; Gunseli, Meeter, and Olivers 2014; Vogel and Machizawa 2004). In this section, CDA was used to track WM reactivation for LTM information when the information is re-experienced in anticipation of external attentional guidance is present (search task) and absent (no search-only recognition task). In addition, despite not being our main hypothesis, we performed contralateral alpha-band (8-12 Hz) power suppression, which is an index of spatial selective attention within WM (Foster et al. 2016; Günseli et al. 2019; Hakim et al. 2019). This analysis aided us to understand to what degree participants allocate attention to the target item and suppress the other, irrelevant information.

At the beginning of the experiment, participants learned 24 real-life objects from randomly picked 2 animate and 2 inanimate categories from a pool of 36 object categories. Later, participants were tested for these memory items. The main experimental phase, where we record the EEG, started with the re-presentation of the target object on a specific side (either left or right in line with CDA requirements) along with a different real-life object. To use as a baseline for the reactivation of LTM in WM reflected in CDA levels, participants performed main tasks with novel information in addition to the studied information. The main tasks were performed in blocked design: 1) search task (external attentional demand is present), 2) simple recognition task (external attentional demand is absent). In the search task, par-

ticipants aimed to find the target object around a circle-shaped display comprising 6 objects (1 target; 5 distractors from the same category). In the simple recognition task, participants were expected to respond to whether the probe matched the target.

When information is re-experienced, it may trigger a WM representation automatically (Schurgin et al. 2018). Therefore, CDA was expected to be observed for both tasks. Considering that deactivating this WM representation via suppression could be more effortful (Anderson et al. 2004; Feldmann-Wüstefeld and Vogel 2019) with the additional cognitive load in anticipation of external attentional guidance, individuals might avoid going through the effort of such suppression. This avoidance might result in larger WM reactivation for search tasks. Further, a visual search study has shown that people rely on a more detailed representation of the target item when surrounding distractors resemble the target object in the search display compared to the search displays that do not contain the target item category (Schmidt and Zelinsky 2017). Therefore, we hypothesized that the WM reactivation for information stored in LTM would be more robust for anticipating external attention demand vs. mere recognition. Consequently, the CDA level was expected to be higher for the search task than the recognition task. Although previous studies have focused on search and recognition tasks performed with novel information (Gunseli, Olivers, and Meeter 2014; Schmidt and Zelinsky 2017; van Driel et al. 2017), daily life often necessitates performing search and recognition tasks with daily life objects. By including learned daily-life objects in the study, we contributed to the literature with better simulation of real-life as it should be done more often in cognitive psychology studies. Also, this study shed light on the WM and LTM interactions by examining the role of WM for search and recognition tasks which are frequently used in daily life. To preview our main findings, contrary to our expectations, the CDA level for the recognition task was higher compared to the search task. Results showed that flexible interaction between WM and LTM is not specially adapted to external attentional demand.

## 2.2 Method

### 2.2.1 Participants

Before data collection, we registered our stopping rule to the Open Science Framework (OSF) (<https://osf.io/hwz64>). We declared that after the first 20 participants,

Bayes Factor (BF) analysis will be performed in every 5 participants, and we will stop collecting data when BF10 reaches 10 in favor of a meaningful difference between search and recognition conditions. 34 students under the age of 35 from Sabanci University participated in an exchange for course credits. We excluded some participants due to ocular and recording artifacts and reached aimed BF10 in 25 participants (13 women; 12 men). All reported having a normal or corrected-to-normal vision and no neurophysiological disorder. After artifact rejection, participants with lower accuracy scores (lower than %60) and less than 100 trials per condition were excluded. This study was conducted according to the rules of the Declaration of Helsinki and approved by Sabanci University’s Research Ethics Council (SUREC) approved the ethics.

### **2.2.2 Stimuli**

There were 2 semantic categories (animate, inanimate) and 2 memory sub-categories (new, studied) of real-world objects. We included new object categories to compare the CDA level between new and studied objects. For visual purposes, all objects ( $1.5^\circ \times 1.5^\circ$ ) were resized, and non-transparent pixels were equalized. Participants viewed the computer screen from a 75 cm distance. The background color was gray (RGB = [128 128 128]). The black fixation dots (RGB = [0 0 0]) stayed on the screen across the whole trial ( $0.3^\circ \times 0.3^\circ$ ) and were used as feedback at the end of the trial. For incorrect answers, the color of the fixation point was red (RGB = [256 0 0]), and for correct answers, it was green (RGB = [0 256 0]). The experiment was prepared in the Psychophysics Toolbox in MATLAB (Mathworks, Natick, MA).

### **2.2.3 Procedure**

The experiment consisted of 3 phases: study, test, and the main experimental phase. In the study phase, the 24 objects (2 animate; 2 inanimate categories) were shown 3 times and stayed on the screen for 2000 ms.

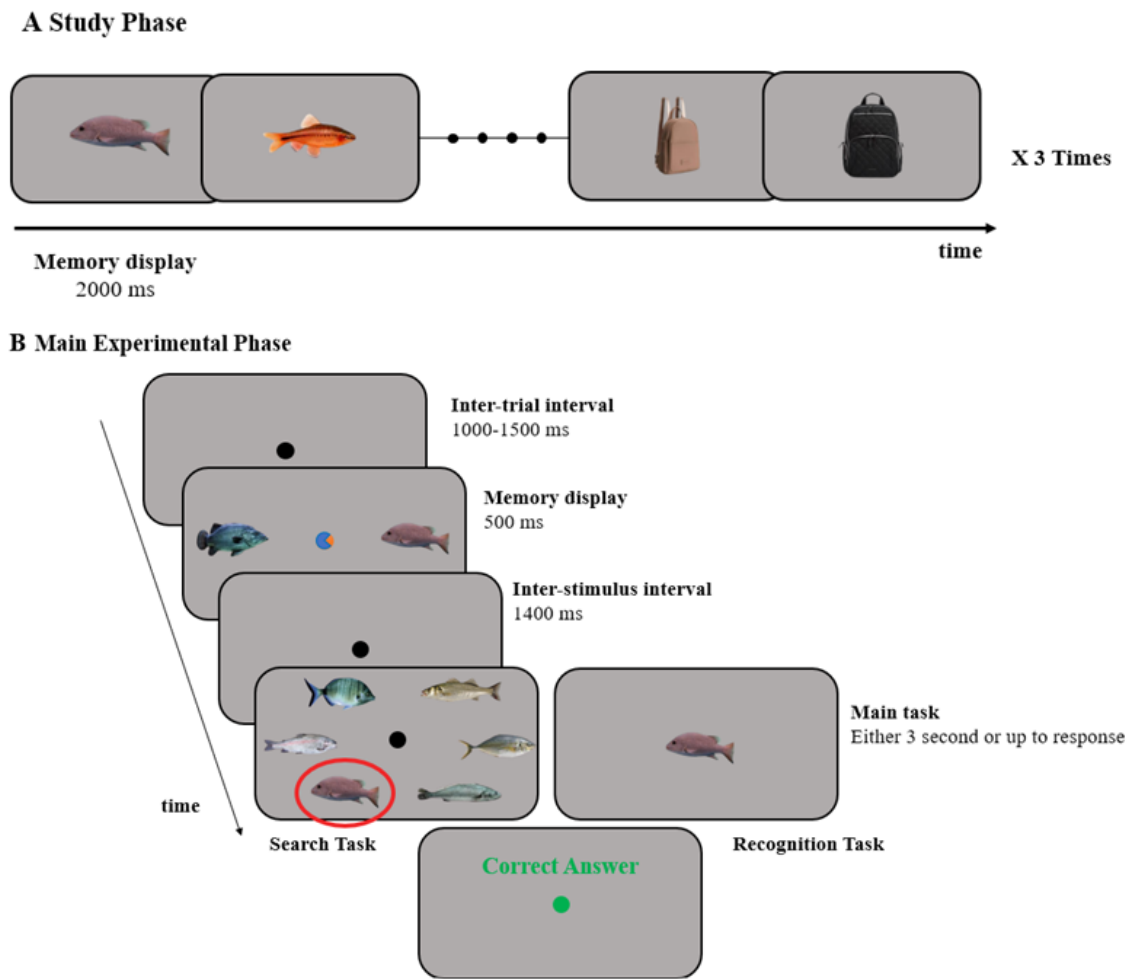
After the study phase, participants proceeded to the test phase. This phase was critical for understanding whether participants encode objects in LTM. First, two objects from the same category (one of the targets; one was the lure object) were located above and below the black fixation point. Objects stayed on the screen until a response. Here, participants indicated the correct memory object by pressing either the up or down arrow on the keyboard. For incorrect answers, the target

object was framed with a green rectangle, while the lure object was framed with a red rectangle. For correct answers, only the target object was framed with a green rectangle. Participants performed the study phase by taking random objects for each trial and were expected to give 4 correct answers in a row for each object. The test phase continued until participants met the criteria.

In the main experimental phase, participants performed either a search task or a recognition task across different blocks with the studied and novel information. For each task, each trial began with the presentation of a randomly jittered black fixation point (1000-1400 ms) followed by a memory display. Memory display contained 2 objects (one target; one lure object) from the same category, located on the left and right side of the black fixation point, aiming to balance visual input. The target object was indicated with a colored cue. Following the memory display, a black fixation point was shown in the inter-stimulus interval for 1400 ms. Following the interval, either a search display or recognition probe appeared.

Before each block, participants were informed about which task they were about to perform. In the search task, there were 6 images (1 target object and 5 random objects from the same category) that were randomly located around an imaginary circle. Participants indicated whether the target is on the left or right side of the search display with left and or right arrow keys on the keyboard. In the recognition task, they responded to whether the test object matched the target object. The maximum response time was allowed as 3000 ms. After the response, feedback on accuracy was given for 1000 ms after each trial. A red fixation point was shown for incorrect answers, while a green fixation point was presented for correct answers. At the end of each block, participants received overall accuracy along with motivational sentences.

Figure 2.1 Example trial flow



(A) The time course of events in the study session. (B) The time course of events in the experimental session.

## 2.2.4 Trial Distributions & Block Design

The experimental design was a 2 x 2 factorial, with two within-subject factors: x 2 conditions (search, recognition) and x 2 types of information (studied, novel). In total, there were 4 types of blocks in the experiment. Participants completed 1) a search task with the studied information (named “Search-Studied” in the following parts); 2) a recognition task with the studied information (“Recognition-Studied”); 3) a search task with novel information (“Search-Novel”); 4) recognition task with novel information (“Recognition-Novel”).

Each condition repeated for 4 times, making a total of 16 sequential blocks. The

order of the blocks was counterbalanced across participants. Participants completed 192 trials for all conditions. The stimulus pool contained 36 object categories (18 animate; 18 inanimate). Randomly, 2 animate and 2 inanimate object categories were selected for the study session. The rest of the object categories used for block types include novel information. For each object category, there were other sets of 24 objects randomly selected for the search task (5 objects were selected to be placed on a search display along with the target object) and recognition task (1 object was selected for incorrect answers). At the beginning of each block type, participants completed a short practice session to familiarize participants with different block types.

## 2.3 Results

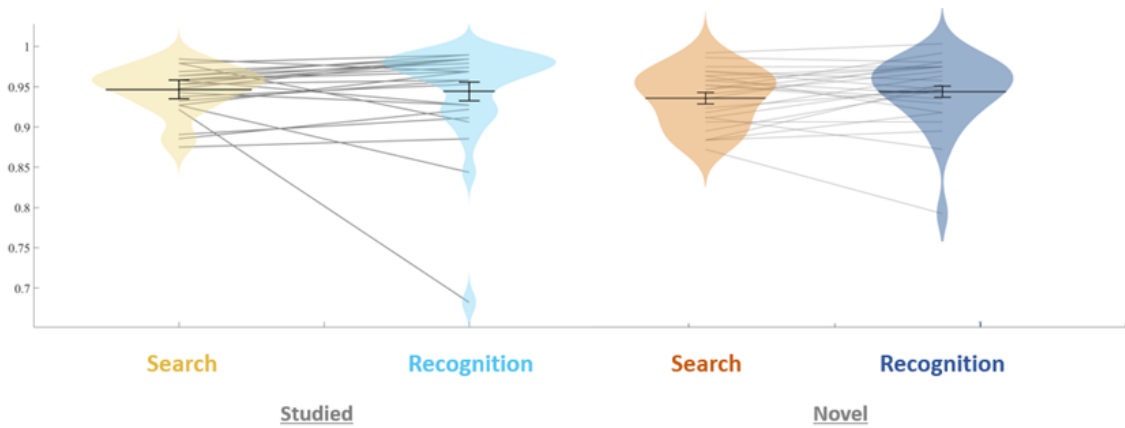
### 2.3.1 Behavioral Results

There were 4 conditions: Search-Studied, Recognition-Studied, Search-Novel, Recognition-Novel. Since our hypothesis is mainly about the external attentional demand difference between conditions, we focused on comparison of search and recognition tasks within the studied and novel information.

Participants understood the instructions well and performed well on each condition (Search-Studied:  $M = 0.95$ ,  $SD = 0.03$ ; Recognition-Studied:  $M = 0.94$ ,  $SD = 0.07$ ; Search-Novel:  $M = 0.93$ ,  $SD = 0.03$ ; Recognition-Novel:  $M = 0.94$ ,  $SD = 0.04$ ). Average accuracy for search and recognition tasks did not differ between conditions (Search-Studied vs Recognition-Studied:  $d = 0.20$ ,  $BF_{10} = 0.21$ , 95% HPD =  $[-0.37, 0.40]$ ,  $t(24) = 0.18$ ,  $p = 0.86$ ; Search-Novel vs. Recognition-Novel:  $d = 0.17$ ,  $BF_{10} = 0.38$ , 95% HPD =  $[-0.59, 0.17]$ ,  $t(24) = -1.15$ ,  $p = 0.26$ ). Figure 2.2 shows the average accuracy.

The RT results showed that participants are faster to respond in recognition tasks (Recognition-Studied:  $M = 0.59$ ,  $SD = 0.08$ ; Recognition-Novel:  $M = 0.59$ ,  $SD = 0.09$ ) compared to search tasks (Search-Studied:  $M = 0.67$ ,  $SD = 0.12$ ; Search-Novel:  $M = 0.67$ ,  $SD = 0.12$ ) for studied and novel information (Search-Studied vs Recognition-Studied:  $d = 0.82$ ,  $BF_{10} = 75.47$ , 95% HPD =  $[0.31, 1.21]$ ,  $t(24) = 4.01$ ,  $p = 0.0004$ ; Search-Novel vs Recognition-Novel:  $d = 0.67$ ,  $BF_{10} = 15.19$ , 95% HPD =  $[0.19, 1.05]$ ,  $t(24) = 3.36$ ,  $p = 0.003$ ). Figure 2.3 shows average RTs.

Figure 2.2 Main task accuracy results



Accuracy results for each conditions were shown for all participants. Error bars represent one standard error normalized for within-subjects variance.

Figure 2.3 Main task reaction time results



Reaction time results were shown for all participants in each condition separately. Error bars represent one standard error normalized for within-subjects variance.

### 2.3.2 Electrophysiological Recordings and Analysis

Electroencephalogram (EEG) data were acquired at a sampling rate of 1000 Hz from 32 sintered - AG/AgCl electrode positions based on the 10/20 System and from both earlobes (used as reference). These electrodes were attached to an elastic cap (actiCAP, Brain Products). To detect blink artifacts and eye movements, the

vertical electro-oculogram (VEOG) was recorded located 1 cm above and below the right eye, and the horizontal EOG (HEOG) was recorded with electrodes (F7 and F8) extracted from the electrode set 1 cm away from the outer corners of the eyes. VEOGs are used to detect vertical eye movements, while HEOGS are used to detect horizontal eye movements. Reference electrodes (TP9 and TP10) were attached to the mastoids, with TP9 as the online reference. Electrodes placed across scalp are listed as follows: “Fp1, Fp2, F3, F4, Fz, FC5, FC6, FC1, FC2, C3, C4, Cz, CP5, CP6, CP1, CP2, P7, P8, P3, P4, Pz, PO7, PO8, PO3, PO4, O1, O2, and Oz”.

The EEG analysis was conducted using MATLAB R2023a (Mathworks, Natick, MA), in conjunction with the EEGLAB toolbox (version 2021.1; (Delorme and Makeig 2004), the ERPLAB toolbox (Version 8.30; (Lopez-Calderon and Luck 2014), and custom scripts. The data underwent filtering using an IIR Butterworth filter with a band-pass range of 0.01-40 Hz, using the `pop_basicfilter.m` function of ERPLAB. Offline re-referencing was carried out by averaging the signals from the right (TP10) and left (TP9) mastoids. Long epochs were defined from -2.5 to 3.9 ms, with memory display as the reference point (time 0). For artifact rejection, an additional short epoching was conducted from -0.5 to 1.9 ms (until the end of the inter-stimulus interval). Epoching was performed using the `pop_epoch.m` function of EEGLAB. Manual visual inspection was used to identify and discard recording artifacts (muscle noise, slow drifts, saturation, and blocking) and ocular artifacts (eye movements and blinks). Artifact rejection was performed blindly. In addition to the trials containing such artifacts, incorrect behavioral responses were excluded from further analysis. Datasets with less than 100 trials per condition were also excluded from the analyses.

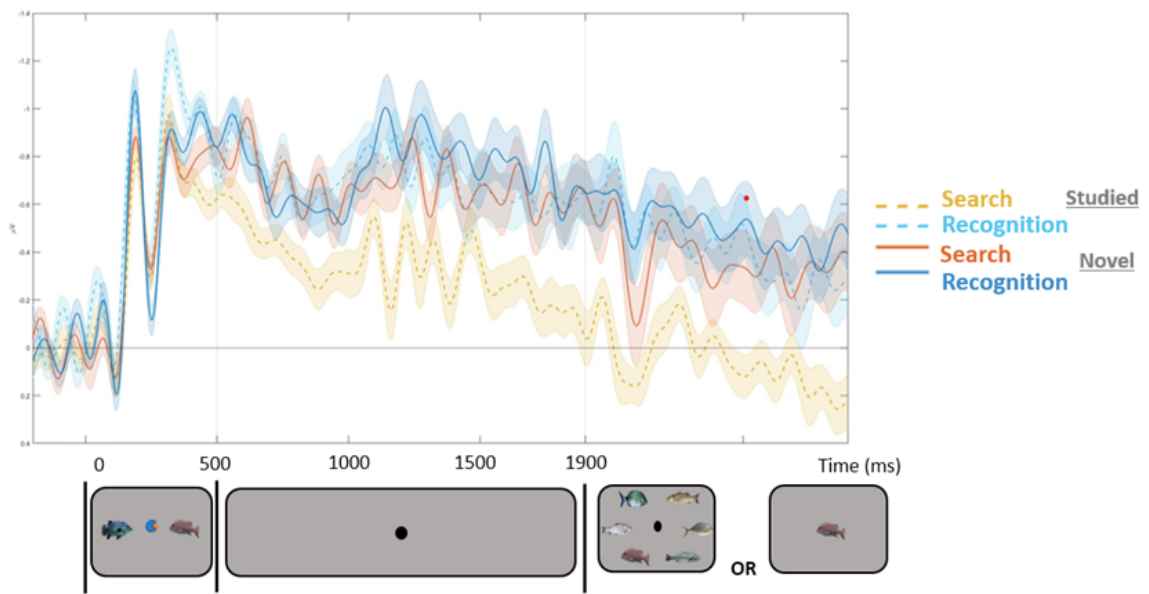
### **2.3.3 Contralateral Delay Activity**

To measure WM involvement, we tested contralateral delay activity (CDA). When participants are directed to attend specific object on the specific side of the screen, if the item is stored in WM, due to the properties of the visual system, our contralateral activity on the occipital electrodes, which is on the contrary side of the target objects, is higher than the ipsilateral activity, which is the corresponding hemisphere of our brain to the target object. In the presence of the contralateral delay activity, we can claim that the information is preserved in WM. CDA is not only sensitive to working memory storage (Gunseli et al. 2018; Gunseli, Meeter, and Olivers 2014; Vogel and Machizawa 2004), but also it is sensitive to the number of items stored in WM (Hakim et al. 2019).

The baseline period for the CDA analysis was 300 ms prior to the onset of the stimulus, and the CDA analysis was computed for the time interval between 500 ms and 1900 ms, corresponding to the inter-stimulus interval between memory display and main tasks. The CDA (contralateral delay activity) was computed using the PO3/4, P3/4, P7/8, PO7/8, and O1/2 channels by measuring the voltage difference between corresponding electrodes located contralateral and ipsilateral to the position of the target object (Gunseli et al. 2018; Gunseli et al., 2014; Hakim et al., 2019; Vogel and Machizawa, 2004). To perform Bayesian paired samples t-test between conditions, CDA was averaged across 700 ms to 1700 ms. Figures 2.4 and 2.5 show CDA results.

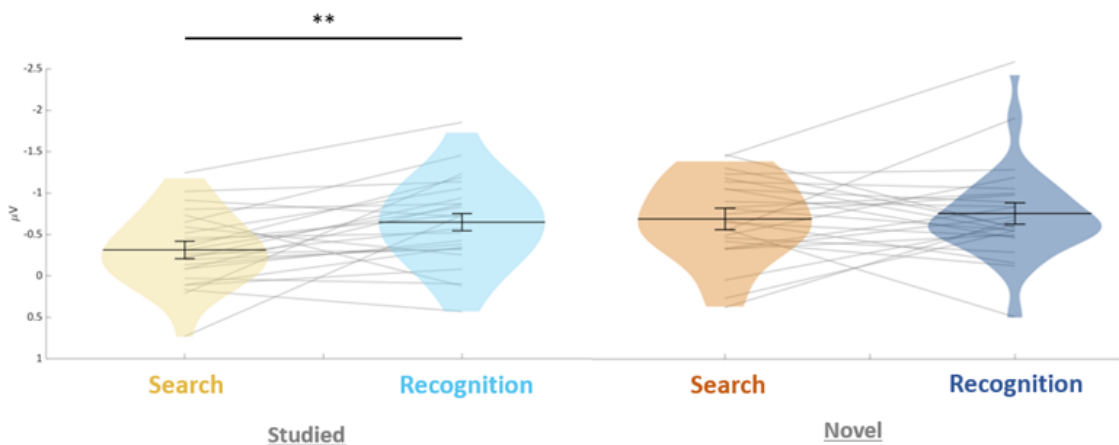
Performing one-sample t-test and BF analysis, we observed that the CDA was present for all conditions (Search-Studied:  $M = -0.34$ ,  $SD = 0.47$ ,  $d = -0.72$ ,  $BF_{10} = 24.11$ , 95% HPD =  $[-1.09, -0.23]$ ,  $t(24) = -3.58$ ,  $p = 0.002$ ; Recognition-Studied:  $M = -0.70$ ,  $SD = 0.57$ ,  $d = -1.24$ ,  $BF_{10} = 8856.80$ , 95% HPD =  $[-1.69, -0.64]$ ,  $t(24) = -6.19$ ,  $p < 0.001$ ; Search-Novel:  $M = -0.67$ ,  $SD = 0.51$ ,  $d = -1.32$ ,  $BF_{10} = 22101.68$ , 95% HPD =  $[-1.79, -0.71]$ ,  $t(24) = -6.60$ ,  $p < 0.001$ ; Recognition-Novel:  $M = -0.74$ ,  $SD = 0.61$ ,  $d = -1.21$ ,  $BF_{10} = 6551.94$ , 95% HPD =  $[-1.67, -0.62]$ ,  $t(24) = -6.05$ ,  $p < 0.001$ ), meaning that participants relied on WM for studied and novel information in each task. For novel information, the CDA did not differ between the tasks (Search-Novel vs Recognition-Novel:  $d = 0.10$ ,  $BF_{10} = 0.24$ , 95% HPD =  $[-0.28, 0.46]$ ,  $t(24) = 0.52$ ,  $p = 0.606$ ). This finding is in line with a previous work that used novel information only, suggesting that WM activity for storing novel information does not differ depending on the anticipated task type (van Driel et al. 2017). For studied information, the CDA was higher for the recognition task compared to search task (Search-Studied vs Recognition-Studied:  $d = 0.64$ ,  $BF_{10} = 10.25$ , 95% HPD =  $[0.16, 1]$ ,  $t(24) = 3.18$ ,  $p = 0.004$ ). This finding suggests that participants reactivated previously studied memories less when anticipating attentional guidance demands than recognition demands.

Figure 2.4 CDA results - waveforms



The waveforms for the CDA for all conditions are shown in different colors (Search-Studied: dashed-yellow; Recognition-Studied: dashed-blue; Search-Novel: solid-orange; Recognition: solid-blue). Under the CDA graph, experimental flow corresponding to time points in the CDA analysis was shown. The CDA was averaged for the time window corresponding to the inter-stimulus interval between the memory display and main task probe.

Figure 2.5 CDA results



Solid lines show average CDA values for each participant. The error bars indicate the

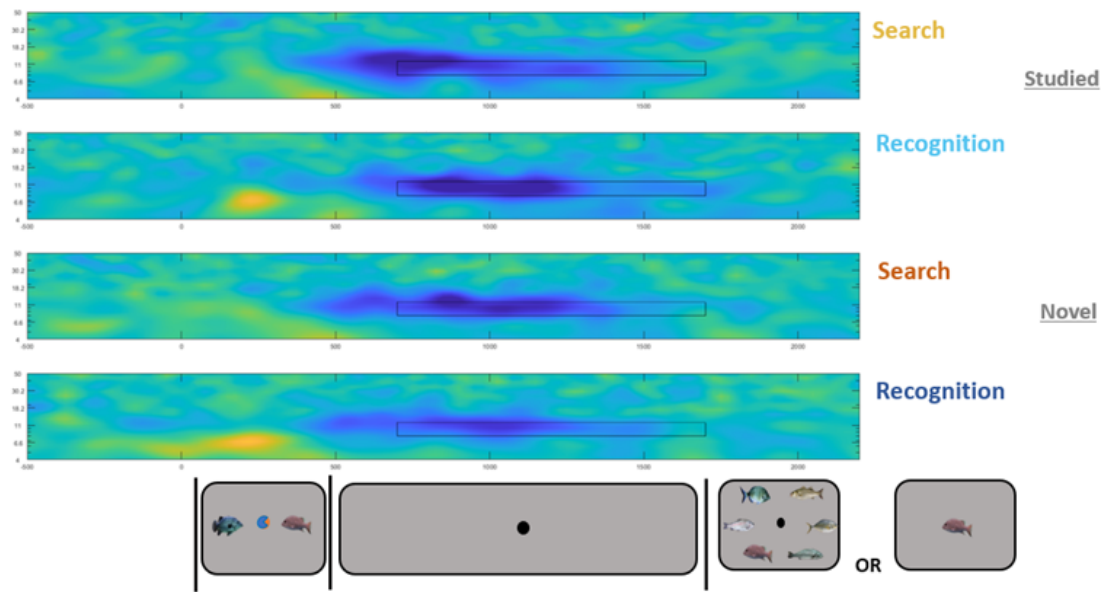
standard error of the mean for the within-participant condition differences (Search-Studied vs Recognition-Studied; Search-Novel vs Recognition-Novel).

### 2.3.4 Lateralized Alpha-band (8-12 Hz) Power Suppression Analysis

Alpha oscillations (8-12 Hz) reflect the deployment of visuospatial attention to presented targets and visual working memory maintenance (Crespo-Garcia et al. 2013; Schack, Klimesch, and Sauseng 2005). The presence of lateral alpha-band power suppression indicates that individuals attend to a target item located on the specific side of the screen and suppress the other item located on the contrary side. For analysis purposes, the clean trials, and the same channels (PO3/4, P3/4, P7/8, PO7/8, and O1/2) we used for the CDA analysis within the same window of interest (700 – 1700 ms) were used in the analysis. Similar to the principles of the CDA, lateralized power suppression refers to the quantification of the discrepancy between the dB-normalized power values of contralateral (opposite) and ipsilateral (same) brain regions. The power values were averaged within the alpha-band frequencies ranging from 8 to 12 Hz.

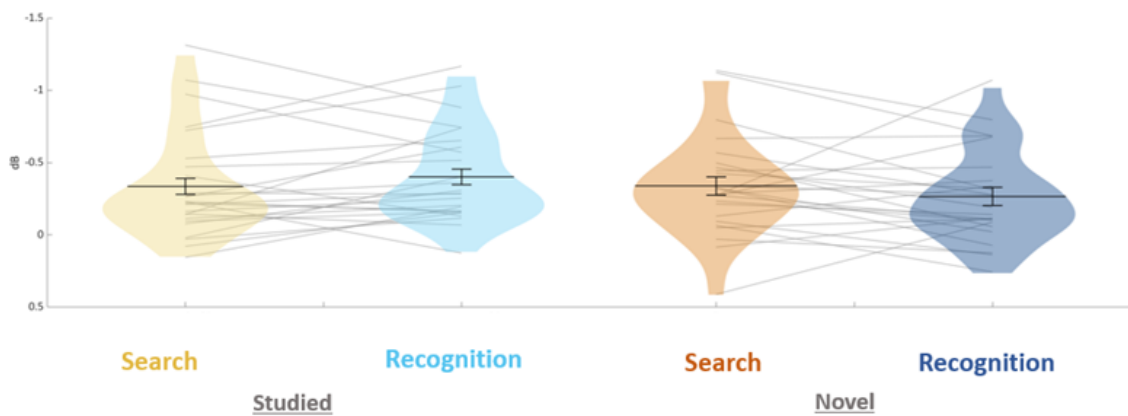
Results have shown that lateral alpha power suppression was observed in all conditions (Search-Studied:  $M = -0.37$ ,  $SD = 0.37$ ,  $d = -0.90$ ,  $BF_{10} = 200.87$ , 95% HPD = [-1.31, -0.38],  $t(24) = -4.53$ ,  $p < 0.001$ ; Recognition-Studied:  $M = -0.40$ ,  $SD = 0.32$ ,  $d = -1.24$ ,  $BF_{10} = 9111.59$ , 95% HPD = [-1.70, -0.64],  $t(24) = -6.20$ ,  $p < 0.001$ ; Search-Novel:  $M = -0.34$ ,  $SD = 0.35$ ,  $d = -0.98$ ,  $BF_{10} = 473.03$ , 95% HPD = [-1.40, -0.44],  $t(24) = -4.90$ ,  $p < 0.001$ ; Recognition-Novel:  $M = -0.26$ ,  $SD = 0.32$ ,  $d = -0.82$ ,  $BF_{10} = 81.22$ , 95% HPD = [-1.22, -0.31],  $t(24) = -4.18$ ,  $p < 0.001$ ), meaning that participants allocated spatial selective attention on the target item while suppressing the lure object on the memory probe. There was no difference in lateral alpha suppression between search and recognition tasks for studied or novel information (Search-Studied vs Recognition-Studied: ( $d = 0.24$ ,  $BF_{10} = 0.40$ , 95% HPD = [-0.16, 0.59],  $t(24) = 1.19$ ,  $p = 0.24$ ).; Search-Novel vs Recognition-Novel: ( $d = -0.23$ ,  $BF_{10} = 0.39$ , 95% HPD = [-0.59, 0.16],  $t(24) = -1.17$ ,  $p = 0.25$ ). Together with the CDA, these results suggest that participants reactivate memories less when anticipating visual search though they might be directing an equal amount of internal attention.

Figure 2.6 Lateral alpha power suppression results



Lateralized alpha power suppression is shown for each condition separately. An example of an experimental flow is shown in accordance with the time window used in the calculation of alpha power suppression. Specifically, alpha power was averaged across the time window indicated with the grey rectangle for analysis purposes.

Figure 2.7 Average lateral alpha power suppression values for each participant



Solid grey lines represent the averaged power suppression values for each participant. The error bars indicate the standard error of the mean for the within-participant condition differences.

## 2.4 Discussion

In this section, we examined the effect of attentional guidance demands on flexible anticipatory interactions between WM and LTM with EEG. Contrary to our expectations, results have shown that the reactivation of LTM in WM is stronger for recognition task than search task. There are some possible explanations for the higher WM reactivation for the recognition task compared to the search task: First, participants might be preparing for the search display with more passive memories to protect the memories against interference that might arise due to sensory recruitment during WM activation. The search might be anticipated to be more disruptive because the search display contains 6 objects while the recognition display contains only one object. Second, participants might be preparing for attentional guidance via passive memories given that previous studies found faster and more efficient visual search for attentional templates stored in LTM vs in WM (eg, (Carlisle et al. 2011; Gunseli, Meeter, and Olivers 2014); also indirectly suggested by (John Robert Anderson 2000; Gordon D. Logan 1988). In lateral alpha suppression analysis, we did not find convincing evidence for differential internal attention to memories stored for attentional guidance and recognition for studied and novel objects. The result for the novel objects is not in line with a previous work that found stronger internal attention to items stored for a search task (van Driel et al. 2017). One possibility is that stronger internal attention is needed to store real-life objects despite the upcoming task. In any case, we found differential patterns of results for the CDA and alpha. This is in line with previous work which obtained dissociations between WM storage and attention (Hakim et al. 2019). Together, these results highlight that internal attention and activation in WM are distinct mechanisms.

### 3. GENERAL DISCUSSION

Although the involvement of WM for retrieving, manipulating, and storing information in LTM has been investigated extensively (Fukuda and Woodman 2017; Meiran, Cole, and Braver 2012; Mızrak and Oberauer 2022; Oberauer 2002; Vo et al. 2021), the exact role of WM remains unclear. While WM is the default buffer for accessing information retrieved from LTM for some studies (Fukuda and Woodman 2017; Vo et al. 2021), for another study, WM reactivation is preserved mainly for particular task demands, supporting the strategic involvement of WM to store information (Mızrak and Oberauer 2022). Considering the experimental procedure of past studies, the difference in the involvement of WM might be dependent on the information used in the tasks and task demands. For example, Fukuda et al. (2017) used spatial information in the recognition task, while Mızrak et al. (2022) focused on verbal material in serial recall task. Therefore, an adaptive account of the role of WM on LTM might be the key to reconciling the seemingly contradicting results in the literature.

In the present work, we tested this anticipatory role of WM for information in LTM by examining behavioural and neural markers of WM and LTM for different information types and task demands. In the first section, we measured WM reactivation of LTM information for mental integration and recognition. The results revealed that information in LTM reactivated in WM for mental integration task and not for recognition task. The second section investigated the effect of external attention guidance with search and recognition tasks. The findings suggested that the reactivation of LTM in WM occurs for search and recognition tasks, meaning that LTM reactivation is not affected by the external attentional guidance demands. The WM ‘re’activation that we found in our studies might be established via 1) stronger neural responses in networks representing a given representation (Funahashi 2017; Fuster and Alexander 1971; Goldman-Rakic 1995); 2) better tuning of their response profiles (Ester et al. 2013; Foster et al. 2016), or, 3) stronger interregional connectivity across multiple brain regions (Hampson et al. 2006; Sauseng et al. 2007).

The contrasting results between the first and the study in this work might be explained by the fact that they use different types of information, which is in line with previous works that used these types of information (e.g., (Fukuda and Woodman 2017; Mızrak and Oberauer 2022), two studies in this thesis use different types of information. While the first study focuses on spatial information, the second study uses daily life objects. The difference in the findings for recognition task for different information types points the findings that WM is not mainly specialized in one area in the brain, but rather it coordinates the activity of several brain regions working together as a network, such as frontoparietal brain regions, including the prefrontal, cingulate, parietal cortices, and even the midbrain and cerebellum (Chai, Abd Hamid, and Abdullah 2018). It is still not known precisely in which regions and how the working memory takes the role for the cognitive processes for LTM information. It is possible that spatial information in LTM is represented in the retrosplenial cortex (RSC), which is a key part for encoding and storing spatial information (Czajkowski et al. 2014), and consequently WM reactivation might not be involved in the operations in RSC. Instead, it might be possible that passive LTM presentation for spatial information is guided directly from RSC without further need for WM. Regarding object processing, WM shows activation for structure and functional organization of the brain regions involved in the ventral pathway (occipital-temporal regions) (Ren et al. 2019). It might be possible that WM reactivation is established via stronger interregional connectivity across the ventral pathway for information in LTM. Further research can explore how WM is reactivated for information stored in LTM across various regions of the brain using fMRI.

Second, the representation of the LTM information is different in the studies. LTM information in the second study is re-presented in the memory display, which intrinsically triggers WM representations (Schurgin et al. 2018). Considering the short amount of time between the memory display and the main task probes, participants might prefer to continue holding information in WM. On the other hand, in the first study, participants accessed LTM information retrieving the location associated with the retrieval cue. Given the additional cognitive load of retrieval compared to encoding (Heitz et al., 2008), participants might prefer to hold LTM information in a relatively passive state rather than fully activate it in WM since reactivation in WM is metabolically costly (Kool et al. 2010).

In summary, our behavioral and EEG results shed light on the role of working memory for information in LTM and lead us to the following conclusions: (1) information in LTM reactivated in WM mental integration task, emphasizing the importance of WM for manipulating information retrieved from LTM, (2) WM reactivation of LTM information is not dependent on external attentional guidance demands, (3)

Performing the recognition task with different types of information might have resulted in contrasting findings for WM reactivation. Overall, our work suggests that the role of WM on LTM information is contingent on information type and task demands, suggesting that the employment of WM for LTM information is flexible and anticipatory.



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