# ATTENTION MODULATES RETRIEVAL PERFORMANCE AND MAINTENANCE OF REPRESENTATIONS IN VISUAL WORKING MEMORY

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#### ABSTRACT

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We live in an age of information overload. To optimize our daily task performance, we need to adopt and discard information critically. However, the mechanisms of focusing on taskrelevant information and ignoring irrelevant information, and in which states the relevant and irrelevant information are maintained in mind, are largely unknown. The current work investigated how multiple memory objects are retained and manipulated by objects' task relevances and selective attention. In a mixed-design working memory (WM) study, the reliability of a spatial cue that predicted the recall of one of two memory colors was manipulated in three conditions (i.e., nonpredictive: 50% reliable; predictive: 75% reliable; deterministic: 100% reliable) as within-subject factor, and selective attention was directed externally by a precue and internally by a retro-cue as between-subject factor. Depending on the cue reliability, participants memorized one or both of two distinct memory colors. They conducted a series of visual searches concurrently during the WM delay, followed by a test in which participants had to recall one of the memory colors. We used the memory-based attentional capture effect for intervening visual searches during the delay as a behavioral proxy to represent the strength of memory representations. Therefore, our experimental design allowed us to examine the attentional effects on both WM retrieval performance and internal memory representations.

The results of the present experiments suggested that guiding attention externally could better improve memory retrieval performance than guiding attention internally and manipulating information priority through cue reliability could also influence memory performance, but not in a linear manner. Importantly, external/internal attention and task relevance could modulate memory representations, both quantitatively (in the degree of memory representation strength) and qualitatively (all-or-none). However, their modulation effects were not as strong as that on the retrieval performance, suggesting a dissociation (partially or wholly) between our measures of memory representation strength and final retrieval performance. We also investigated the temporal changes of strength of memory representations during the WM delay and provided partial support to the claim that guided attention protects memory representations from degradation or volatility.

This study, to our knowledge, is the first to systematically investigate the effects of cue type and reliability on WM performance at the retrieval and memory representations during the maintenance. We also demonstrated the potential of using memory-based attentional capture effect to represent memory representations. Future researchers may want to use this paradigm in more research scenarios.

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#### **CHAPTER 1**

## **GENERAL INTRODUCTION**

Working memory refers to the cognitive ability used to store and manipulate information in mind, over a time span of seconds, for future use. It operates on "internal" information that is not immediately available to the senses (Chun, Golomb, & Turk-Browne, 2011). You might remember a shopping experience with your parents at a grocery store when you were a child, your parents wanted you to grab a bottle of milk and a carton of eggs, and you ran away repeating the words "milk", "eggs" in your mind, so you did not forget the important job with which you had been entrusted. At that time, you had never heard the term working memory, but you had used it to help to achieve goals in your daily life.

WM is a core component in a variety of high-level cognitive functions such as language, reasoning, problem solving, and abstract thought (Baddeley, 1992). It has different components, including encoding, maintenance, and retrieval of information. Of these components, the ability to maintain information in the absence of sensory input has always been an active topic of WM research. Unlike long-term memory, in which capacity is theoretically unlimited, working memory is said to be capacity-limited across domains, such as auditory (Prosser, 1995), visual (Luck & Vogel, 1997), verbal (Chen & Cowan, 2009), and even tactile (Katus, Müller, & Eimer, 2015). This dissertation focused on how the limited capacity of WM is prioritized in the visual domain (visual working memory, VWM).

Because of the limited capacity of WM, it is particularly important to utilize the WM resources efficiently. For example, one might strategically guide attention to prioritize memory contents which are mostly task-relevant, and deprioritize contents which are less relevant by diverting attention away from them. Providing a cue to indicate which memory information is

more task-relevant has been proven to be an effective way to guide attention both externally and internally. Many WM studies have revealed the effects of cues on memory recall performance, while few studies have focused on investigating how cues alter the state of item representations in VWM. This current work aims to reveal the effects of cues on both memory recall and item state in VWM.

In this pursuit, in the following sections, I started by discussing the conceptual changes in the limited capacity of VWM. These included changes from models claiming that WM only holds a fixed, small number of items to models claiming limited WM resource can be distributed flexibly among all maintained items. I then discussed how mechanisms involved in WM are subserved by selective attention. Thirdly, I discussed the approaches to select information into and within WM. One of the important factors that impact the cueing effect on memory performance, namely the reliability of the cue, was also discussed. Fourthly, I reviewed both neuroimaging and behavioral methods to measure the WM item states. Lastly, I laid out the hypotheses and predictions of this work.

#### The Limited Capacity of VWM

In his seminal paper, George Miller (1956) suggested that people can recall a maximum of approximately seven randomly ordered, meaningful items or chunks, which was described as "the magical number seven plus or minus two". However, this observation was made based on three different kinds of tasks, which Miller later thought might be a "pernicious, Pythagorean coincidence." (Cowan, 2015). A wealth of subsequent studies have also yielded different results; for example, in a hallmark study, Luck and Vogel (1997) found that VWM capacity is limited to only three or four items. A similar capacity limit was also observed in verbal working memory (Gilchrist, Cowan, & Naveh-Benjamin, 2008). Cowan (2001) summarized various results and

made the point that there is a "new magic number four". Whether the magic number is four or seven, both models assume WM is determined only by the number of items, while the complexity of individual items does not incur additional load upon WM capacity. For example, Luck and Vogel (1997) found that memory capacity for objects defined by a single feature (e.g., color or orientation) was equivalent to capacity for multi-feature objects (e.g., colored lines of varying orientations). This slot conceptualization of WM is thus all or none: each slot stores information with equal precision, and once the object limit is reached, no further items can be stored in WM.

The evidence for this classical slot view has primarily arisen from tasks with the change detection paradigm (Ma, Husain, & Bays, 2014). These tasks used a discrete or categorical stimulus set and asked participants to detect the presence of changes among an array of items by making binary responses (same or different). However, not all studies using change detection paradigms were consistent with this classical slot view. For example, Alvarez and Cavanagh (2004) found WM capacity varied across different classes of stimulus materials, and that capacity was related to the complexity of each object stored in memory. Therefore, they posited that the capacity is actually information-limited instead of object-limited. Awh, Barton, and Vogel (2007) later directly countered Alvarez and Cavanagh's result by suggesting the limiting factor in Alvarez and Cavanagh's study (2004) was the probability of errors during the comparison stage of their WM task (i.e., sample-test similarity) rather than the object complexity per se. When they controlled the sample-test similarity, they found there is a fixed number of items represented in visual WM, regardless of the complexity of these items.

This slot/object-limit account of WM capacity was further challenged with alternative paradigms of assessing fine-grained information about the quality of remembered items (Wilken

& Ma, 2004; Zhang & Luck, 2008). In this continuous-report measure, participants were asked to remember an array of items (e.g., colors or orientations). After a delay, they were asked to recall the identity of one of the items by picking up the memoranda from a probe wheel that contains a circularly-wrapped, continuous space (e.g., color space or orientation space). The distance between the response and the actual stimulus was considered as a measure of memory precision. Compared with the change detection paradigm, these continuous-report tasks provide a more sensitive measure of memory recall performance because they do not just make binary (i.e., same or different) response about participants' recall performances, which could be insensitive to small differences in memory resolution and miss important memory information. Importantly, using this methodology, researchers have found the precision of memory responses decreases as the number of items increases, even if the memory array size is well below the classical item limit of slot models, and the memory performance is still above chance when the object limit is exceeded (Bays, Catalao, & Husain, 2009; Bays & Husain, 2008).

Based on the results of this continuous-report paradigm, some researchers revised the slot model. For example, Zhang and Luck (2008) proposed the "slot+averaging" model. This model still predicts a fixed upper limit, however, distinct from the classical model, it suggests that when the limit is not exceeded, some items with high-resolution memory representations are stored in more than one slot. The slot+averaging model, however, has been challenged by the continuousresource models of WM (Bays & Husain, 2008; Bays et al., 2009; van den Berg, Shin, Chou, George, & Ma, 2012; Wilken & Ma, 2004). These models do not assume a strict capacity limit; therefore, subjects do not wholly fail to store items when the capacity limit is reached. Instead, they predict that any response will contain some information about the identity of the probed memory item. Because the WM resource is finite, the fidelity with which an item is stored in

memory is determined by the fraction of the memory resource dedicated to that item (Bays & Husain, 2008).

Even though the resource models do not predict a fixed number of memory items that can be stored, many sources of errors, such as misbinding errors (i.e., misbinding features within memory items so that the wrong features are attributed to probed items) (Bays et al., 2009), encoding errors (Bays et al., 2009), or interference from other items (Oberauer & Lin, 2016), could contribute to the observed limited capacity of working memory. The revised slot model can actually also be considered as a discrete or quantized resource model (Ma et al., 2014) because it assumes discrete slots can be shared out between items. Overall, resource models and the revised slot model provide a much more flexible framework than the classical slot model.

In recent years, a growing body of evidence has indicated that memory resources can be voluntarily controlled and unevenly distributed so that prioritized objects receive more resources and are stored with enhanced precision compared to other objects (Yoo, Klyszejko, Curtis, & Ma, 2018). This resource allocation mechanism makes the WM system operate more effectively and has real-life advantages.

Consider a situation in which you are a salesperson, and you are introduced to a group of potential clients. If someone shows interest in your product after talking with you, you might want to dedicate more WM resources to memorize that person's information, even though you know every client could be valuable. That is, the complexity of natural scenes makes even distribution of resources often unlikely and impractical, and in many cases, some objects are more salient or more relevant for the current task goals than others, and therefore receive more resources. One fundamental question that can be asked is, what are the underlying mechanisms

that might be governing the WM resource allocation? Selective attention<sup>1</sup> has been nominated as a prominent candidate. In the next section, I will explain how selective attention plays different roles in modulating WM resources.

## WM and Selective Attention

Previous studies have suggested that appropriately directing attention to the most taskrelevant stimuli during maintenance can partly overcome VWM capacity limits (Lepsien, Griffin, Devlin, & Nobre, 2005; Sligte, Scholte, & Lamme, 2008). It is well known that increasing WM load leads to decreased performance (Sternberg, 1966); however, orienting attention to the items in WM could attenuate this effect of load. Lepsien and colleagues (2005) replicated the classic finding that increasing memory load (from two to four) was accompanied by increased response time (RT) and decreased memory accuracy. However, when attention was directed to the to-be-probed item during maintenance, the loading effect was significantly smaller than that when attention was not manipulated. Other studies suggested that when VWM capacity was not exceeded (below four objects), orienting participants' attention to items within VWM can enhance memory performance (Astle, Summerfield, Griffin, & Nobre, 2012).

Another line of research suggested that improper allocation of attention to task-irrelevant stimuli would diminish WM performance by using its limited capacity to store unimportant information (Vogel, McCollough, & Machizawa, 2005; Zanto & Gazzaley, 2009). For example, Zanto and Gazzaley (2009) presented four sequential apertures of dots to participants, two of them were colored and stationary, and the other two were moving and gray. In the two-item WM task, participants only needed to pay attention to two color hues or two motion directions while

<sup>&</sup>lt;sup>1</sup> Kiyonaga and Egner (2013) considered selective attention as the prioritization of processing geared at external representations. In this dissertation, I expanded their definition and used it to refer to any attentional processing that selects WM information either externally or internally.

ignoring other features. In the four-item task, participants had to remember both colors and both motion directions. Electroencephalography (EEG) signals for both to-be-attended and to-beignored memory stimuli were recorded. Their results revealed that the spectral marker of memory load during maintenance was comparable between four-item trials and low-performance two-item trials, suggesting that lower performance was probably due to irrelevant items entering WM.

Moreover, individuals with low WM capacity are thought to adopt suboptimal attentional selection during the encoding phase of a visual WM task (Linke, Vicente-Grabovetsky, Mitchell, & Cusack, 2011). Studies of aging effects suggest that the suppression-specific attention deficit in ignoring irrelevant information could be associated with impaired WM performance (Gazzaley, Cooney, Rissman, & D'Esposito, 2005; Gazzaley et al., 2008). For example, Gazzaley et al. (2008) subdivided the older population based on their working memory performances and revealed that compared with the younger adults, the lower-performing group exhibited a selective deficit in suppressing irrelevant information, whereas the higher-performing group did not show a suppression deficit. To conclude, these results suggest that selective attention could confer benefits and costs to items in VWM; that is, proper control over attention can boost memory performance while improper control over attention can deteriorate memory performance.

Some neural studies and WM models suggested that selective attention supports the active maintenance of information in WM. For example, Sreenivasan and Jha (2007) suggested that selective attention can be recruited to bias sensory processing against distractors in support of WM maintenance. They recorded event-related potential (ERP) signals while participants were performing a delayed-recognition task for faces and shoes. They found the N170 ERP

component, which is face-sensitive, was attenuated in the context of congruent WM (both memory item and intervening distractors during the delay were faces) relative to incongruent WM (memory item was shoe while the distractors were faces). The behavioral performance also suffered in the congruent WM condition relative to the incongruent condition, suggesting the attenuated perceptual processing of distractors during WM maintenance was associated with impaired memory performance.

Other studies employed the multistep delayed-recognition task and provided direct support to the claim that attention can function as a mechanism for selecting and prioritizing WM representations. For example, in a functional magnetic resonance imaging (fMRI) study, Lewis-Peacock and colleagues (Lewis-Peacock, Drysdale, Oberauer, & Postle, 2012) presented two memory items concurrently to participants. After the offset of memory items, the first cue was presented, indicating which memory item was relevant for the first probe. After the first probe, a second cue appeared to indicate whether the same item (repeat trials) or the previously deprioritized item (switch trials) would be tested in the following probe. Using a decoding algorithm, the authors found that after the first cue, the classifier evidence for the prioritized item was elevated, whereas evidence for the deprioritized item dropped to the baseline level. Interestingly, if the second cue was a switch cue (i.e., previously deprioritized item would be probed), internal attention would be switched to the previously deprioritized item, thereby enhancing the classifier evidence for that item, while evidence for the previously prioritized item dropped to baseline. If, in contrast, the second cue was a repeat cue, classifier evidence for the already-selected memory item remained elevated, and the evidence for the deprioritized item remained indistinguishable from the baseline.

Many WM models also acknowledged the interplay between WM maintenance and selective attention. According to the "component processes" view of WM, information maintenance in WM is considered to be a product of interactions between various cognitive processes, and attention is understood to be the cornerstone of these varied processes (Eriksson, Vogel, Lansner, Bergström, & Nyberg, 2015). Postle (2006) expressed a similar idea that WM functions are produced through the coordinated recruitment of multiple brain systems (e.g., sensory-, representation-, and action-related systems) via flexibly deployable attention.

According to state-based models of WM, attention is used to establish a higher state of accessibility for perceptual and long-term memory (LTM) representations (D'Esposito, & Postle, 2015; Eriksson et al., 2015). For example, Cowan's (1998) embedded-processes model of WM described two distinct states of WM: a temporarily activated subset of information in LTM (activated LTM), and a capacity-limited state termed the focus of attention (FoA) within the activated LTM. The activated LTM is less accessible than representations in the FoA but more accessible than general LTM representations. Cowan proposed the FoA can contain approximately four chunks of information, and the items that are in the FoA can be transferred into activated LTM when attention is diverted away. On the other hand, the information stored in the activated LTM can be easily transitioned into the FoA once attention is switched back. Oberauer's three-embedded-components model (Oberauer, 2002, 2009) extended Cowan's model. It posited three components in WM: the activated part of LTM, the region of direct access, and a single-item focus of attention. The activated part of LTM and the region of direct access were similar to Cowan's activated LTM and four-item FoA. However, Oberauer further suggested the existence of a narrower focus of attention that serves to select only one item or chunk at a time within the region of direct access. Consequently, these three components can

also be referred to as three levels of selection in WM (Oberauer, 2019): (1) selecting information to be in WM, establishing the current memory set; (2) selecting a subset of information within the memory set; (3) selecting a single item from the memory subset. Despite some terminology and conceptual differences, these state-based models all posited that information in WM is maintained in an elevated state of activation via attention.

The time-based resource-sharing model of WM (Barrouillet & Camos, 2012) emphasizes the importance of attention as it assumes the two main functions of WM (i.e., the temporary storage and the processing of information) are both fueled by attentional resources. This model proposes that attention contributes to memory maintenance through refreshing WM representations, and WM will suffer from a time-related decay as soon as the attention is diverted away. Importantly, it also assumes the WM function is limited by a central bottleneck that only allows one central process at a time. Thus, once accessory tasks occupy the attention, memory traces' refreshments will be prevented, since no attention for refreshment is available. However, attention sharing can be achieved through rapid and frequent switching between processing and maintenance.

Together, previous studies have both empirically and theoretically demonstrated that WM could be related to attention as a selection mechanism. To maximize the use of finite WM resources, attention can selectively process sensory information that is most likely to be task-relevant at encoding or alter the activation status of a stored WM representation. In the next section, I discuss how is information selected into and within WM.

#### **Guiding Attention to WM with Spatial Cues**

#### **Selecting Information into WM**

Attention can be deployed to perceptual information at WM encoding, as well as to information already stored in WM. In the former view, attention is taken as a strict gatekeeper to let through some stimuli while blocking others at the entry-level of processing incoming information (Awh, Vogel, & Oh, 2006), or a more flexible logistician that strategically distributes resources at encoding to stimuli in accordance with participants' needs (Dube, Emrich, & Al-Aidroos, 2017). In either case, attention modulates prioritization before stimulus presentation (Gorgoraptis, Catalao, Bays, & Husain, 2011; Griffin & Nobre, 2003; Nobre et al., 2004; Schmidt, Vogel, Woodman, & Luck, 2002; Zokaei, Gorgoraptis, Bahrami, Bays, & Husain, 2011). An effective way to direct observers' attention to incoming information is to use a cueing paradigm (i.e., the pre-cue paradigm) in which a spatial cue appears at or points to a peripheral location. Stimuli appearing at the prioritized location (valid trials) are usually better recalled than those appearing at the deprioritized location (invalid trials) when the cue was predictive (Griffin & Nobre, 2003; Schmidt et al., 2002) or even nonpredictive (Schmidt et al., 2002).

For example, in an early study using pre-cues to orient attention at WM encoding, Schmidt and colleagues (2002) presented participants with a memory array of six colored squares preceded by spatial cues, and asked them to report whether the color of the probe square matched the color of the square that had appeared at the same location in the memory array. One group of participants received a predictive cue, which correctly predicted the location of the probe square on two-thirds of the trials (i.e., 66.7% reliability) while, in the other group, the cue did not give any useful information about which color was more likely to be probed. Their

results suggested that memory accuracy for valid trials was significantly higher than invalid trials in the predictive cue group and, interestingly, a smaller but reliable cue validity effect was observed even when the cue was not predictive. Similarly, Griffin and Nobre (2003) compared the memory for valid and invalid trials with a predictive cue to baseline trials in which no spatial cue was presented. Their results revealed the RT advantage for the valid trials with corresponding memory accuracy cost for the invalid trials relative to baseline trials. This suggests that there are both benefits for prioritized items and costs for deprioritized items. In addition to the deployment of selective attention to the domain of spatial location, selective attention can also be directed to features (Gorgoraptis et al., 2011; Zokaei et al., 2011) and objects (Serences & Yantis, 2006). This dissertation work focuses on spatial cues.

Crucially, to what extent the pre-cue facilitates encoding into WM can be modulated by the strength of attentional demands. A common way to regulate attentional demands is to control the reliability of the cue strategically. Cue reliability refers to the proportion of time that a cue correctly predicts the to-be-probed item. Studies have suggested that assigning different cue reliabilities prior to memory array would influence the way WM encodes items (Yoo et al., 2018).

Yoo and colleagues (2018) asked participants to remember the locations of four dot targets. Prior to the presentation of the memory array, participants were presented with a pre-cue, which indicated the probe reliability (i.e., 0.6, 0.3, 0.1, and 0) at each location. When probed, participants were instructed to saccade to the remembered dot location, and the Euclidean distance between the actual and reported target location was computed. Their results revealed that the response error decreased linearly with increasing priority. However, when they further investigated what strategy participants used to allocate resources in response to different cue

priorities by comparing different computational models of resource allocation. Interestingly, they found that participants underallocated resources to high-priority targets and overallocated resources to low-priority targets, relative to the actual probe reliabilities. In their view, participants with limited resources allocate their resources more equally than proportional, and people adopt this strategy to minimize expected loss, where loss is defined as estimation error to a power. Therefore, it is evident that people can use cueing information to filter or prioritize information at encoding; however, this controlled process is not perfect: the allocation of the attentional resource might not be in line with the actual attentional demands.

Several other studies systematically manipulated the cue reliabilities presented simultaneously with the memory array to study how information is selected at encoding (Dube et al., 2017; Emrich, Lockhart, & Al-Aidroos, 2017; Klyszejko, Rahmati, & Curtis, 2014). For example, Emrich et al. (2017) presented probabilistic spatial cues varied from 8.25% to 100% concurrently with the memory array and demonstrated that the effect of cue reliability on WM recall performance was best fit by a power-law function. It is worth mentioning that the design of presenting cue concurrently with memory array is not equivalent to pre-cue since it does not involve the same preparation process as pre-cue; however, these findings may still shed some light on the influence of pre-cue reliability on memory process at encoding.

Some neural mechanisms have been proposed to interpret the pre-cueing effects. Orienting attention to a specific region or a particular feature increases the neural activity of the corresponding neural region, and this attentional effect can even persist without the presence of any stimuli in the specific region or any particular feature (Chawla, Rees, & Friston, 1999; Fazekas & Nanay, 2017; Giesbrecht, Weissman, Woldorff, & Mangun, 2006; Reynolds, Pasternak, & Desimone, 2000). Giesbrecht et al. (2006), for instance, found elevated pre-

stimulus activity in location- and color-selective regions of the visual cortex in response to cues to attend to a location or color, suggesting that activity in visual cortex can be modulated in preparation for an upcoming target stimulus. Moreover, this enhanced pre-stimulus activity correlated with increased behavioral performance on both the spatial and feature tasks.

The biased competition account (Desimone & Duncan, 1995) also provides a useful theoretical framework to understand this pre-stimulus attentional modulation. According to this account, changes in pre-stimulus activity could be generated by top-down excitatory signals, originating from control areas in frontal and parietal cortex, that bias neurons representing the selected stimuli. As a consequence of this biasing signal, the attended stimulus is given a competitive advantage for limited neural resources, resulting in a higher level of processing of the attended items relative to unattended ones.

#### **Selecting Information within WM**

On the one hand, knowing ahead of time that a subset of information is more likely to be probed is helpful for participants to prioritize relevant information requiring access to their limited WM. On the other hand, knowing which already encoded item has become more or less relevant is equivalently useful so that important information can be strengthened or protected from degradation and/or interference, while irrelevant information can be forgotten or weaken. A widely used approach to select or prioritize individual items from the set currently held in WM is to use the retro-cue paradigm in which a cue is presented during the retention interval of a WM task.

The retro-cue effect was first described independently by two research groups (Griffin & Nobre, 2003; Landman, Spekreijse & Lamme, 2003). For example, Griffin and Nobre (2003) presented three kinds of cues to participants in a VWM task: the pre-cue, the retro-cue, and the

neutral cue (giving no cueing information). In the retro-cue condition, participants were given spatially informative cues (80% reliable) 1500-2500 ms after the memory array was presented. Participants were then asked to decide whether the probed stimulus had been present in the memory array. The authors found similar validity benefits and invalidity costs in the retro-cue condition as found in the pre-cue condition: it led to a robust advantage/disadvantage in detection performance in valid/invalid trials relative to trials without cues.

In recent years, the retro-cue paradigm has attracted considerable interest, and this retrocueing effect was repeatedly observed in many different studies. First, the retro-cue could be presented either centrally or peripherally, and the cueing effects were observed regardless of their positions (Matsukura, Cosman, Roper, Vatterott, & Vecera, 2014; Shimi, Nobre, Astle, & Scerif, 2014). Second, in addition to the ubiquitous use of spatial retro-cues, validity effect were observed for color or shape retro-cues (Heuer & Schubö, 2016; Li & Saiki, 2015), verbal cues (Hollingworth & Maxcey-Richard, 2013), auditory cues (Backer & Alain, 2012), and even tactile cues (Katus, Andersen, & Müller, 2012; Katus & Eimer, 2015). Last, the retro-cue has been demonstrated in both children (Shimi et al., 2014) and aging groups (Gilchrist, Duarte, & Verhaeghen, 2016; Newsome et al., 2015; Souza, 2016). Overall, these studies, across different domains and different population groups, demonstrate that retro-cue is a powerful tool enabling researchers to investigate how information stored in WM is selected for processing.

It is well known that retro-cue can guide attention to the prioritized item within WM and thereby improve memory performance for that item; however, it is still debating whether the retro-cue benefits arise at the expense of performance when the deprioritized item is tested. For example, according to the slot+averaging model of WM, the retro-cue benefit can be explained by the assumption that the prioritized item is assigned more than one slot and gains precision

through averaging across slots. In consequence, fewer slots are available to the deprioritized item. The resource framework of WM assumes the retro-cue effect engages a shift of limited memory resource from the deprioritized item to the prioritized item, thereby the amount of resource for the prioritized item is increased, while the resource for the deprioritized item is decreased. These two models both predict benefits for the prioritized items should be accompanied by costs for the deprioritized items held in WM. In contrast, the three-embeddedcomponents model of WM implies that selecting an item into the focus of attention by retro-cue enhances that item's accessibility but does not damage the representations of other items stored in the region of direct access.

Empirical evidence also differed regarding the influence of retro-cue towards the deprioritized items. Studies reported costs in recall for deprioritized items mainly used highly reliable cues (Oberauer & Lin, 2017; Pertzov, Bays, Joseph, & Husain, 2013) or even 100% reliable cues (Williams, Hong, Kang, Carlisle, & Woodman, 2013). For example, in the study by Pertzov et al. (2013), participants were shown four tilted bars and were asked to recall the exact orientation of a probe bar at the end of a variable retention interval. As compared with the baseline (no-cue) trials, they found the deviations between reported orientation and the target orientation was smaller on valid trials but larger on invalid trials when the retro-cue was 70% reliable. Furthermore, the deviations increased over the retention interval on both no-cue and invalid trials, but not on the valid trials, suggesting focusing attention on a memory item protects it from degradation over time.

It is hard to measure the cost for the deprioritized item behaviorally in cue condition with 100% reliability since the deprioritized item was not eventually probed. Williams and colleagues (2013) overcame this difficulty by probing those items surprisingly and mainly focused on

participants' performance on the first deprioritized item. In the task, they asked participants to memorize two colors and then presented a directed-forgetting cue to instruct participants to drop one of two colors. Participants reported the target color by clicking the best matching color on a color wheel. They analyzed participants' responses using a quantitative model that fitted a von Mises distribution. They found that the probability that the to-be forgotten representation was still in memory was only approximately 1%, suggesting it was simply removed from the WM store. A better approach to evaluate the deprioritized item might be using neuroimaging methods. In a WM study with EEG recording, Wolff, Jochim, Akyurek, and Stokes (2017) asked participants to remember two memory orientations, and during the delay interval, a 100% reliable retro-cue was provided to indicate which orientation would finally be tested. Their results showed that the decodability of the prioritized item was above the chance level, while the deprioritized item showed no evidence of decoding, again suggesting it was removed from WM storage as instructed (see also Ester, Nouri, & Rodriguez, 2018).

A few studies used a double-cueing paradigm and reported that focusing on one prioritized item in WM does not damage the performance for other items (Lepsien & Nobre, 2006; Rerko & Oberauer, 2013). Rerko and Oberauer (2013), for example, compared color WM performance in single-cue trials and two-cue trials. In the single-cue trials, the cue was always valid. In the two-cue trials, the second cue was always valid, but the first cue was always invalid. They matched the retention intervals to prevent participants from anticipating the number of cues in a trial. The logic was that if focusing on the earlier prioritized item is detrimental to other deprioritized items, then when one of the previously deprioritized items is later prioritized, the performance for that item should not be as good as that in single-cue trials. Their results showed that the two kinds of trials resulted in similar memory accuracy, implying that the deprioritized

items are remained unimpaired in WM even when the task does not require them. However, the lack of costs for deprioritized items in these studies might be due to participants' memory strategy. Participants might try to keep all memory items after the first cue because they did not know whether the cue was valid or not.

Gunseli, van Moorselaar, Meeter, and Olivers (2015) summarized the studies that produced conflicting results and proposed that the reliability of the cue may be a factor that partially explains the inconsistency in cue-related costs. In a retro-cue study with two cue reliabilities, Gunseli et al. (2015) instructed participants to remember four concurrent orientations, then a retro-cue with 80% reliability or 50% reliability was presented. They observed the retro-cue benefits (i.e., memory performance was better than that of neutral cue condition) on valid trials in both 80% reliable and 50% reliable cue conditions; however, invalidity costs were found only when the retro-cue was 80% reliable, but not when the retro-cue reliability was 50% reliable. Therefore, when the cue is relatively less reliable, participants chose to maintain deprioritized items in anticipation of potentially being probed on them. Nevertheless, when they realize the chance of deprioritized items being tested is negligible, they can devote most of the resources to the prioritized items and remove the deprioritized items.

While there is evidence that the reliability of the cue can influence the benefits and costs of retro-cue effect, a remaining question that has not been addressed in the retro-cue literatures is whether the retrieval performances for valid and invalid trials change with cue reliabilities. That is, does the performance for valid trials increase when the prioritized item is more relevant to the task, and/or decrease for invalid trials when the deprioritized item is less relevant? A straightforward model may assume that memory performance scales with cue reliability. However, a recent study suggested that it may not be that simple. Dube, Lumsden, and Al-

Aidroos (2019) manipulated cue reliability to be deterministic (i.e., 100% reliable) or probabilistic (i.e., 70% reliable), and compared their cueing effects on memory performance and memory states. Their results suggested that, although participants could use the cue to prioritize WM as suggested by the better performance in valid trials than in the invalid trials with the 70% reliable cue, there was no significant performance difference in valid trials between the 70% reliable cue and 100% reliable cue. Intriguingly, they also measured the mental states of prioritized items with a visual search task. The logic was that if the prioritized item is kept in an active state, it can bias the visual search. The results showed that memory item prioritized with 100% reliability did bias attention in the visual search task; however, the 70% reliably prioritized item did not, suggesting a 70% reliable cue was not sufficient to make a WM representation active. Overall, these results suggested that even though WM retrieval performance can be strongly predicted by proportionally distributed WM resources based on cue reliabilities, the relationship may not be monotonical, some more complicated controls can be involved.

Several potential mechanisms have been raised to look closely at the nature of the retrocue effects. For example, Myers, Stokes, and Nobre (2017) suggested a model in which retrospective prioritization acts in multiple steps: First, orienting towards and selecting the prioritized item in the WM store. This process could strengthen the association between a prioritized location, assuming a spatial cue is given, and the features of the object presented at that location, which in turn reduces noise or increases activation in the neural population representing the prioritized object. Following selection, the prioritized representations can be transformed into an active state in the service of upcoming task demands. Importantly, once this prioritization and transformation are complete, sustained attention to the sensory representations is no longer strictly necessary: attention can be withdrawn from the prioritized item towards

another task or another WM representation. The idea that the prioritized information undergoes a transformation in its representational state coincides with some other influential theories, such as the state-based models of WM (Cowan, 1998; McElree, 1998; Oberauer, 2002), which conceptualize information in WM as existing in various states of activation established by the allocation of attention.

Souza and Oberauer (2016) provided a comprehensive summary of key mechanisms that may be responsible for the retro-cue effect in WM performance: (1) attending to internal representations can protect them from time-based decay (i.e., the protection account); (2) the retro-cue can help to remove the deprioritized items to free up WM capacity to process the prioritized items (i.e., the removal account); (3) attending to an item in WM leads to a stronger binding of that item to its context, not a shift of memory strength from other items to the attended item, therefore, the strength of other item-context bindings are not affected (i.e., the attentional strengthening or refreshing account); (4) the retro-cue takes effect ahead of testing by temporally separating the retrieval and decision making processes, thereby allowing more time to accumulate evidence for the relevant items before feeding it into the decision process (i.e., the retrieval head start account); (5) the retro-cue facilitates comparisons between prioritized WM representations and subsequent memory probes (i.e., the prioritization for comparison account); (6) the retro-cue leads to protection of the prioritized items from perceptual interference at test, whereas, deprioritized items are not protected and, hence, are impaired by interference (i.e., protection from perceptual interference).

Among those hypotheses (for detailed descriptions of those hypotheses, see Souza & Oberauer, 2016), the former four focus on the roles of retro-cues in the maintenance stage of WM, while the latter two focus on the retrieval stage. It is important to note that these

hypotheses are not mutually exclusive. For example, the protection from perceptual interference and decay accounts can be by-products of the attentional strengthening account: the retro-cue may strengthen the memory trace of the prioritized items, making them more robust to interference at test or time-based decay. These six putative accounts on their own only offer partial explanations to the retro-cue effect, but together they may be able to delineate a complete picture of the retro-cue effect.

## **Comparing the Pre-cue and Retro-cue**

From the studies I have reviewed so far, it seems behavioral effects and neural mechanisms are comparable for both pre- and retro-cues. This observation is also consistent with the hypothesis that common mechanisms are involved in selection in internal and external attention (Kiyonaga & Egner, 2013). However, several studies have directly compared pre- and retro-cues to investigate the relationship between external and internal attention in WM tasks, and revealed mixed results (Fang, Ravizza, & Liu, 2019; Griffin & Nobre, 2003; Janczyk & Reuss, 2016; Li & Saiki, 2015; Myers, Walther, Wallis, Stokes, & Nobre, 2015; Nobre et al., 2004; Robison & Unsworth, 2017; Shimi et al., 2014). For example, Nobre et al. (2004) directly compared the effect of pre-cues and retro-cues on WM performance, and they found that accuracy and RT of retro-cues with 80% reliability were equivalent to those associated with precues. Furthermore, their fMRI analyses also suggested that these two cue types share common neural substrates to a large extent. However, Li and Saiki (2015) applied a similar paradigm as in Nobre et al. (2004) and suggested that pre- and retro-cue shared a common mechanism when attention was directed via a spatial cue, but not when attention was directed by color cue. Specifically, pre-cues generated greater color cue effect than retro-cues, indicating that the efficiency of cue types might be mediated by cue properties. One possible explanation for the

greater color versus location pre-cue effect is that location cue effects are mainly mediated by facilitation via prioritized location, whereas color cue effects are mediated by both facilitation via prioritized color and suppression via deprioritized color (Li & Saiki, 2015).

More recent studies reported differences in attention-related WM mechanisms even when cueing was location-based. Robison and Unsworth (2017) recruited a large group of participants (176 participants) and asked them to complete a four-item change detection task with a neutral cue, pre-cue, and retro-cue. Both spatial cues were 100% reliable. They compared accuracy for different cue types and revealed that accuracy was significantly higher for pre-cued trials compared to retro-cued trials, and both spatial cue trials resulted in higher accuracies than neutral trials. Myers and colleagues (2015) pointed out that previous studies directly comparing pre-cues and retro-cues have not controlled some important nuisance factors; for example, the two cue types appeared at different times within a trial sequence. They proposed a new visual WM task to overcome this shortage and equate all aspects of stimulus presentation between cueing conditions. Their results suggested that both pre- and retro-cues with 70% reliability improve WM performance, but again, the overall performance was significantly higher for items from pre-cue trials. They also collected EEG data while participants performed the task and examined cue-evoked event-related potential (ERP) markers of attentional orienting for both cue types. In general, they found pre- and retro-cues differentially modulated these ERP profiles. For example, retro-cues had significant larger early directing attention negativity than pre-cues, which indicated a rapid refocusing of attention after retro-cues. Pre-cues evoked the typical lateralized anticipatory response, which is associated with the top-down deployment of anticipatory spatial attention, but retro-cues did not and even led to a significant reversal of this potential.

There may also exist a developmental dissociation between external and internal attention orienting. Shimi et al. (2014) compared pre- and retro-cues with 100% reliability in a change-detection task across three different ages (i.e., 7-year-olds, 11-year-olds, and adults). They found in the pre-cue condition, all three age groups benefited to a similar degree relative to the neutral condition, while in the retro-cue condition, cueing benefits for the 11-year-olds and adults groups were similar, and both better than the 7-year-olds group. The pre-cue benefits were also larger than retro-cue benefits for all groups. Souza (2016) assessed both cue types with 100% reliability in a continuous color reproduction task in both young and old adults. Their results also showed that the benefit of a spatial pre-cue was larger than the benefit of retro-cues in both age groups.

Overall, these results seem to suggest that people are better at utilizing cueing information when the cue is presented in advance of encoding than when it is presented during maintenance. One purpose of this present study is to replicate previous findings by directly comparing the pre- and retro-cueing effects on WM retrieval performance. More importantly, to our knowledge, no study has combined the factors of cue type, namely pre- and retro-cue, and cue reliability to investigate how the effects of cue reliability differ for pre- and retro-cues. The present study is trying to fill this research gap.

#### **Assessing WM Representations**

Many behavioral studies have demonstrated that prospectively and retrospectively cueing attention to memory array improve WM retrieval performance for the prioritized items, while retrieval performance for the deprioritized items suffers from attention being diverted away. The reliability of the cue can modulate the performance benefits and costs of the cueing effect. However, how the prioritized and deprioritized mental representations are maintained during the

retention interval of WM, especially under different cue reliability conditions, has remained largely elusive.

Recent advances in multivariate imaging techniques have allowed for a quantitative assay of the fidelity of internal representations (Ester et al., 2018; Sprague, Ester, & Serences, 2016; Wolff et al., 2017). For example, Ester et al. (2018) applied an inverted encoding model to EEG alpha band (8-12 Hz) activities to reconstruct spatially-specific mnemonic representations, while participants performed a retro-cue WM task. During each trial, participants remembered the locations of two colored discs. When a neutral cue was presented, they observed a gradual decrease in the strength of location-specific representations over time, which echoed the decay account of memory maintenance. When a retro-cue with 100% reliability was presented immediately after the offset of memory discs, location representation for the prioritized disc remained constant across the delay period; however, location representation for the deprioritized disc quickly dropped to 0 (for a similar study in fMRI, see Sprague et al. (2016)). Compared to most behavioral approaches, which only measure the final retrieval outcome (e.g., RT or accuracy), these neuroimaging approaches provide tools for researchers to directly assess the fidelity of internal representations during the memory delay.

It is also possible to investigate mental states of WM items during maintenance in behavioral studies. Previously, I have mentioned that Dube and colleagues (2019) used attentional bias triggered by the content of maintained WM item as a proxy to infer the inner state of the item during maintenance. The idea that the deployment of attention can be biased by information held in working memory is not new. For instance, one early study (Downing, 2000) asked participants to hold a face in mind, then this target face and a novel face were presented simultaneously side by side. After a brief memory delay, participants were asked to perform an

irrelevant discrimination task on a small bracket appearing at the location of the target face (match) or that of the new face (mismatch). Finally, participants needed to respond whether a test face matched the target face. In this task, participants were faster to respond to attention probes (i.e., brackets) at the match location than to probes at the mismatch location. Critically, this speeded response towards the memory-match item was independent of memory object type and intervening attention task. Therefore, maintaining information in WM affected what participants looked at in the attention task. In other words, a memorized object can capture attention (Olivers, 2009).

Evidence for the memory-driven attentional capture mainly comes from visual search studies. In a canonical visual search paradigm, participants are asked to maintain a visual object (e.g., color) in WM, at the end of the trial, their memory for the memory object is tested. The critical manipulation is that they will perform a distinct attention task, typically a visual search task, which is embedded within the memory delay. In this task, the WM object can reappear in the search display surrounding a visual search target (valid/target-related), distractor (invalid/distractor-related), or does not reappear at all (neutral). For instance, if the search task is to search for a tilted line, the tilted line will be a target, the vertical line will be a distractor. A typical pattern of search performance is searching is faster when the memory item surrounds the target and slower when it surrounds a distractor, relative to the neutral condition (Soto, Heinke, Humphreys, & Blanco, 2005; Soto, Humphreys, & Heinke, 2006).

An alternative explanation to the attentional capture effect is this attentional effect may not be driven by WM content, but simply by visual priming, such that mere exposure to the memory item without a memory requirement. Researchers have excluded this explanation by including a viewing-without-remembering control condition (Downing, 2000; Soto et al., 2005;

Soto, Humphreys, & Rotshtein, 2007). In these control conditions, visual search biases were not observed, suggesting bottom-up priming is not sufficient to guide attention in visual search tasks.

Instead of priming, top-down feedback from activated representations maintained in WM is considered as one of the driving forces in biasing attention. Evidence from eye movements (Olivers, Meijer, & Theeuwes, 2006; Soto et al., 2005) suggested that observers directed their fixations more often to locations of objects in the search display matching the contents of WM than to the locations of nonmatching objects, which corroborates the argument that top-down bias exerts influence on visual search. Furthermore, Olivers et al. (2006) demonstrated that when a WM item was not relevant to the task, and observers had no incentive to keep the memory information, content-related attention capture could disappear. Empirically, they found that when the WM item was switched such that participants first completed the memory test and then performed the search task (see also Olivers & Eimer, 2011), the WM item lost its effect on guiding attention. These results suggested this attentional capture can only occur when the item is indeed actively maintained in memory.

Several studies have suggested that once the memory information is actively stored, WM may guide attention in an involuntary manner. These studies (Soto et al., 2005; Olivers et al., 2006) have included an experimental condition in which the WM content only reappeared as an invalid distractor in visual search. Thus it would be beneficial to search performance if participants ignored WM content. However, RTs were still slower for invalid than for neutral trials, indicating participants could not completely prevent bias from the memory item, therefore supporting the theory that attention is automatically captured by WM (Soto, Hodsoll, Rotshtein, & Humphreys, 2008).

However, other studies argued that the impact of WM content on attention can also be strategically controlled (Dowd, Kiyonaga, Beck, & Egner, 2015; Kiyonaga, Egner, & Soto, 2012). Kiyonaga and colleagues (2012) varied the probability that search targets would occur at the locations of WM-matching items. The memory item either always reappeared as valid target (100% valid), or always reappeared as invalid distractor (100% invalid), or reappeared as valid target in half of the trials and as invalid distractor in another half of the trials in one block (50% valid and 50% invalid), or did not reappear at all (100% neutral). They replicated the finding that the 100% invalid condition was slower than the neutral condition. As usual, the visual search was faster overall on valid vs. invalid trials. Importantly, the search process was also faster on the 100% invalid condition than on the 50% invalid condition, suggesting the attention effect can be modulated by voluntary control.

The status of memory representation could impact visual search as well. As Olivers et al. (2011) theorized, WM items can be designated with different status (e.g., active and accessory WM status). Active representations are directly available, while accessory representations are temporarily peripheral to the current mental manipulations. They suggested that accessory representations will not induce attentional biases or, if they will, attentional biases will not be as strong as those induced by active representations. Consistent with this theory, Olivers and Eimer (2011) found that when participants put more effort into maintaining WM information, attentional guidance was stronger. In their study, they manipulated the order in which the visual search task and the memory test were presented. In the so-called fixed order condition, the order was constant (either the *First Search Then Remember* or *First Remember Then Search* condition), while in the mixed order condition, participants were uncertain about the orders, and either order could be implemented. The crucial difference between the *First Search Then*
*Remember* trials in this mixed condition and the fixed condition is that the mixed condition might have a higher demand on memorizing the WM item because participants would also have an expectation for the *First Remember Then Search* to come, and this condition requires more memory involvement. The results showed that the attentional effects in the *First Search Then Remember* trials in the mixed condition were twice as strong as that in the fixed condition.

What can be the possible neural mechanisms underlying the memory-based attentional bias? In the biased competition model (Desimone & Duncan, 1995), competitions among sensory representations are hypothesized to be resolved either through the top-down feedback from parietal and frontal areas or through bottom-up sensory properties like relative stimulus strength. The prefrontal cortex (PFC) may be one of the crucial areas involved in the top-down control of attention that biases sensory processing towards information that is behaviorally relevant (Miller & D'Esposito, 2005). Once the memory information is encoded, neurons in the PFC send feedback to the visual cortex to enhance the activity of the neurons that code the task-relevant features preceding the presentation of the visual search array, enriching the representation of the search template in memory. After the presentation of a search array, memory representation that matches the search template, promoting the selection of matching visual items during visual search.

Given the strong linkage between attentional capture and WM content, one may wonder if this attentional capture effect can be used as an indicator to represent WM representation status. To the best of our knowledge, only a few studies have used the attentional capture to infer WM representations or states. In one of these studies, Dowd, Pearson, and Egner (2017) presented participants with a colored circle and asked them to hold the color in memory. Before

they were tested for their memory of the color, they were asked to search for tilted lines in 12 consecutive visual searches. As in the classical paradigm of memory-based attentional capture, there were three different visual search conditions. In the target-related condition, the tilted line was surrounded by a circle matching the memory color; in the distractor-related condition, the memory color circle contained a distractor. In the neutral condition, the memory color did not reappear in the search display. Again, they showed that search RTs were speeded to target-related trials and slowed by distractor-related trials, relative to neutral trials. Intriguingly, they fed multivariate pattern classifiers with visual search RTs during the WM delay. Across three separate classification methods, patterns of visual search RT data could reliably decode WM color for a single trial. Classifier evidence was also positively correlated with the magnitude of attentional capture, further suggesting that this memory-based attentional capture contains WM information.

Mallett and Lewis-Peacock (2018) replicated and extended Dowd et al.'s (2017) study. They employed a double-cueing paradigm previously used in fMRI and EEG decoding studies (LaRocque, Lewis-Peacock, Drysdale, Oberauer, & Postle, 2013; Lewis-Peacock et al., 2012). They presented two memory items to participants and used two retro-cues (both with 100% reliability) to manipulate the priority of items such that one item would be relevant for the upcoming memory test. Specifically, during the first memory delay, the deprioritized item was only temporarily irrelevant and could potentially be relevant for the second memory test if it was prioritized by the second retro-cue. However, during the second delay period, the deprioritized item was no longer relevant and could be permanently removed from WM. They quantified the effect of attentional capture by calculating the RT difference between target-related and distractor-related visual search trials for both prioritized and deprioritized items. They then

characterized the temporal dynamics of attentional capture by dividing the entire search set into four quartiles during both delays. This method allowed researchers to measure the strengths of both attended and unattended memory representations, particularly in the same memory delay, without the influence of the memory retrieval process. Their results suggested that in the first memory delay, attentional capture for the prioritized item remained elevated most of the time, and attentional capture for the deprioritized item was significant initially, but dropped precipitously, becoming indistinguishable from the baseline. In the second delay period, attentional capture for the prioritized item remained elevated, and attentional capture for the deprioritized item remained elevated, and attentional capture for the deprioritized item remained elevated, and attentional capture for the deprioritized item remained indistinguishable from the baseline. These results were impressively similar to previous neuroimaging decoding results, demonstrating that attentional capture has the potential to unveil the status of internal representations as neuroimaging decoding methods.

Current studies have made substantial progress in understanding the WM representations in the deterministic (i.e., 100% reliable) and dual cue condition. However, few studies have investigated how the probabilistic cues exert influence over item state during WM maintenance. The present work varied the reliability of the cue to systemically explore how modulating the attentional demand can reconfigure the representation state of items in WM. We adopted the method in Mallett and Lewis-Peacock's (2018) work to calculate the memory-driven attentional capture effect and used its magnitude as a behavioral index to represent the strength of WM representation.

#### Hypotheses of the Present Dissertation

In the present study, I am mostly interested in investigating: (1) the mechanism by which WM performance at retrieval and representation during the retention interval are tuned by attentional demand, directed by the reliability of spatial cue; (2) if the strategical control of

attentional demand depends on whether attention is selected externally or internally, directed by pre- or retro-cues. To measure the strengths of mental representations during maintenance and final memory performance, a visual search task was embedded in the delay period of a color memory task. Three evenly spaced cue reliabilities (i.e., 50%: nonpredictive; 75%: predictive but not deterministic; and 100%: deterministic) were manipulated to directly compare the attention-related changes of WM representations and memory retrieval performances under both cue types. I firstly list the hypotheses for WM representations, because it is the most novel part of this study.

Some studies suggested that external and internal attention share common mechanisms (Kiyonaga & Egner, 2013), and exert equivalent influence on memory retrieval performance (Nobre et al., 2004). More findings (Robin & Unsworth, 2017; Souza, 2016) showed that under the same attentional demand (say cues are 100% valid), memory retrieval performance was better when attention was externally guided than internally guided. In a recent study, Fang and colleagues (2019) found that both types of attention could elicit a surround suppression effect, suggesting that WM representations are sensory in nature regardless of how attention is modulated in WM processes. However, even though the characteristics of memory representations might be the same, external attention still exerted larger cueing effect than internal attention.

Some studies have suggested that this external attention advantage may arise from the higher precision of memory item at recall. In these studies, WM retrieval performance was fitted with the mixture model (Zhang & Luck, 2008) and was broken into two variables: guess rate, which represents a proportion of trials that observer remembers nothing about the item and makes random guesses; and precision, which represents the quality of the observer's memory on

trials when the observer is not guessing. It has been reported that pre-cues could reduce the guess rate and increase the precision of memory (Wallis, Stokes, Cousijn, Woolrich, & Nobre, 2015), however, retro-cues primarily reduced guess rate without influencing the quality of memory (Murray, Nobre, Clark, Cravo, & Stokes, 2013; Myers et al., 2015; Wallis et al., 2015). Though other studies also reported that retro-cues could affect both the recall probability (1-guess rate) and memory quality for the prioritized item (Gunseli et al., 2015), memory quality in the pre-cue condition was better than that in the retro-cue condition (Wallis et al., 2015). While the quality of memory item at retrieval does not necessarily reflect the strength of memory representation during maintenance, given their presumably tight relationship, it was hypothesized that external attention results in stronger memory representations during the maintenance than internal attention.

It has been suggested that the strength of mental representation can be determined by the amount of attentional/memory resources dedicated to the memory item, and the resource allocation can be managed by cueing information (Emrich et al., 2017; Ye, Hu, Ristaniemi, Gendron, & Liu, 2016). When a cue has high reliability (e.g., 75% or 100% reliable), participants may devote most of their attentional/memory resources to the prioritized representation; therefore, the strength of prioritized representation could be stronger relative to the deprioritized representation. When a cue has low reliability (e.g., 50% reliable), both prioritized and deprioritized memory items may receive a similar amount of resources, and their representation strengths could be equivalent. We also expected that the strength of prioritized/deprioritized memory representation would increase/decrease with cue reliability overall, however, given that the resource allocation may not vary linearly with cue reliability (de Silva & Ma, 2018; Yoo et al., 2018), the increment or decrement may not be in a linear manner. For example, we may find

for the prioritized memory representation, the representation strengths between 50% and 75% reliable cues are similar to each other because of the imperfect resource allocation, but the strengths between 75% and 100% reliable cues are different. External and internal attention may also exert different influences on the presumed interaction effects between cue reliability and memory priority (prioritized vs. deprioritized). Since we predicted that the internal attention is less flexible at allocating attentional resources, the interaction effect, if existed, may be weaker in the retro-cue condition than in the pre-cue condition.

Another principal aim of this work is to investigate the status (all-or-none) of prioritized and deprioritized WM representations during the WM maintenance in different cue reliability conditions. This analysis provides an alternative perspective to look at the states of memory items qualitatively. Their status was labeled by comparing the magnitudes of attentional capture effects to the baseline level (i.e., no attentional capture effect). If the magnitude of attentional capture effect of one memory item is above the baseline, it is considered actively kept in mind, because it exerts influence on the intervening visual searches. Otherwise, if the magnitude of that item is not different from the baseline level, it is considered lost during the maintenance. We hypothesized that deprioritized items are removed from memory storage when the cue is 100% reliable in both pre- and retro-cue conditions, while the prioritized items are preserved. In the predictive or nonpredictive cue condition, where both prioritized and deprioritized items are likely to be probed, it is inappropriate to drop either item. However, as reviewed above, the status of memory representations might not precisely reflect the attentional demands. For example, theoretically, participants might allocate zero resource to items that have a nonzero probability of being probed (de Silva & Ma, 2018) either strategically or because attention cannot be finely tuned. Therefore, we hypothesized that the memory representations for

prioritized items could be actively stored during the maintenance in both probabilistic cue conditions; however, the memory representations for deprioritized items in the predictive cue condition (i.e., 75% reliable), but not in the nonpredictive cue condition (i.e., 50% reliable), may be fragile to interference or simply expelled from memory storage because the chance of deprioritized items being tested in this condition is very little.

It has been suggested that the strength of mental representations might suffer from timebased decay. However, directing attention to representations can partially counteract this decay (Matsukura, Luck, & Vecera, 2007; Pertzov et al., 2013; Souza & Oberauer, 2016). For example, Ester et al. (2018) found that the fidelity of WM representations decreased with time during storage when an uninformative retro-cue was presented. Conversely, presenting a 100% reliable retro-cue prevented the monotonic decrease of memory information for the prioritized item, but not for the deprioritized item. Our experimental design also allows us to track the possible temporal changes of the attentional capture effects for prioritized and deprioritized items, although not in as high temporal resolution as the EEG decoding method. We hypothesized that the strength of a memory representation decays unless attention is guided to that memory item. When nonpredictive cues are presented, attention is not guided to either of memory items; thus, we may observe decreased attentional capture for both prioritized and deprioritized items during a WM delay. However, in the predictive and deterministic cue conditions, attentional capture may remain elevated for prioritized items but not for deprioritized items, as the attention might be withdrawn from deprioritized items. This temporal change pattern might be more evident when attention is directed externally, as external attention might be more effective at guiding attention.

Both cue type and cue reliability could regulate memory retrieval performance, probably in a similar pattern as they do to the strength of memory representations: (1) pre-cue may result in better performance than retro-cue; (2) participants can volitionally use the cueing information to guide attention. This strategical control can be reflected in the larger performance difference between valid and invalid trials when the cue is more reliable than it is less reliable; however, the control may not be optimal, retrieval performance of memory items could vary with their outcome probabilities, but not in a linear manner; (3) the ability that participants implement cueing information depends on whether attention is directed externally or internally.

Lastly, many of our hypotheses about WM representations are built upon the assumption that the strength of memory representations during maintenance is highly associated with the final memory performance. To directly test this hypothesis, we collapsed data of each trial across cue type and cue reliability, and constructed linear mixed models with attentional captures of prioritized and deprioritized items as predictors and final memory performance measures (i.e., accuracy and RT) as dependent variables to investigate whether memory retrieval performance can be predicted by the states of prioritized and deprioritized mental representations.

### **CHAPTER 2**

### **METHODS**

### **Participants**

Seventy (pre-cue: 35, age:  $19.50 \pm 1.29$  years, 22 females; retro-cue: 35, age:  $19.51 \pm 1.22$  years, 17 females) healthy participants participated in this experiment in exchange for course credit. They were recruited from the Michigan State University community using the SONA system provided by the Department of Psychology. All participants had normal or corrected-to-normal acuity and color vision. Written informed consent was obtained, and the protocol was approved by the MSU Institutional Review Board.

### Design

We used a 3 (cue reliability: 50% reliable, 75% reliable, 100% reliable)  $\times$  2 (cue validity: valid, invalid)  $\times$  2 (cue type: pre-cue, retro-cue) mixed design. Cue reliability and cue validity were manipulated within participants, whereas cue type was manipulated between participants (31 participants for the pre-cue group, 31 participants for the retro-cue group, see Results for exclusion criterion).

#### **Stimuli and Procedure**

Both the pre-cue and retro-cue experiments were programmed in MATLAB (The Mathworks, Natick, MA) with the MGL extension (http://gru.stanford.edu/mgl/) and displayed on a 19-inch LCD monitor (refresh rate: 75 Hz). The stimuli were rendered against a black background. The experiments used a dual-task paradigm, which consisted of a delayed match-to-sample WM task and a visual search task. Each trial began with a white fixation cross centered on a black background for 300 ms.

For the pre-cue condition, a central arrow cue (i.e.,  $\langle or \rangle$ ) pointing either to the left side or right side of the screen was briefly presented (500 ms), indicating which upcoming memory target would likely be probed at recall (Figure 1A). After a short delay of 500 ms, two different colors, pseudorandomly sampled from a pool of six different color combinations (color RGB values: red = 227, 2, 24; blue = 48, 62, 152; green = 95, 180, 46; yellow = 251, 189, 18), were presented on either side of the fixation for 1000 ms, followed by a 1500-ms delay before the visual search task. Each color combination had the same number of trials. For the retro-cue condition, the cue was presented during the WM retention interval (Figure 1B). Two memory circles with different colors (the color combinations were pseudorandomly sampled from the same pool as the pre-cue condition) were presented for 1000 ms after the initial fixation cross. After a 500-ms delay, the retro-cue was presented for 500 ms, followed by another 500-ms delay before the visual search task. In addition to the temporal placement of the cue, the pre-cue and retro-cue conditions also differed in their delays before the visual search task. This setting was used to make sure the time intervals between color memoranda and the visual search tasks were equivalent.

After the retention interval, a four-alternative, forced-choice memory probe array was presented together with an arrow indicator. The arrow could point either to the left or right side of the screen, indicating the location of the color that should be recalled from the previous memory array. The memory probe array consisted of four randomly organized colored rings with numbers inside, and participants were required to report which color ring matched the target color by pressing the corresponding number key as quickly as possible. Participants had up to 3000 ms to make responses, or the program would continue. Visual feedback (500 ms) was presented following all memory responses (i.e., correct or incorrect).

The probed location could be congruent or incongruent with the prioritized location, and the probability of these two directions being congruent across trials was equivalent to the cue reliability. For the deterministic cue with 100% reliability, the prioritized location was always probed at recall. For the predictive cue with 75% reliability, the prioritized location matched the probed location in 75% of the trials. For the nonpredictive cue with 50% reliability, the prioritized and deprioritized locations were equally likely to be the probed. The cue conditions were blocked and counterbalanced within participants. Participants were informed about the cue reliability at the beginning of each block.



**Figure 1. Experimental designs for the pre-cue and retro-cue tasks.** In two experiments, participants were required to hold two items in working memory while performing a sequence of 12 visual search trials during memory delay. These two experiments differed in the cue locations, in the pre-cue experiment (A), a probabilistic cue was given prior to the memory items, while in the retro-cue experiment (B), a probabilistic cue was presented after memory items. (C) a single visual search trial was illustrated.

Embedded within the delay periods of the memory task, 12 successive visual searches were presented (in randomized order for each trial). The goal of these searches is to provide a measure of the status of WM representation during retention. Each visual search presented a central fixation cross for 300 ms, followed by a search array for 300 ms, and then a blank screen until a response was recorded (or up to 1200 ms). Each search array consisted of two colored

circles presented vertically (Figure 1C). One of the circles surrounded a white tilted line (i.e., search target), and another surrounded a white vertical line (i.e., search distractor). The target lines were tilted 45° either to the left or right, and participants were instructed to respond to the orientations of the tilted lines by pressing the left or right arrow key as quickly and accurately as possible. Auditory feedback was provided for 200 ms after erroneous (i.e., time-outs or wrong keypresses) search responses; otherwise, a blank interval was presented for 200 ms before the next visual search task started.

Importantly, the series of twelve visual searches was designed to contain every possible combination of two colors (six variants) and target-distractor arrangements ( $6 \times 2 = 12$ ). This scheme ensured that for either prioritized or deprioritized color in one WM task trial, there would be three target-related searches (the target lines were surrounded by colored circles matching the prioritized or deprioritized memory color<sup>2</sup>), three distractor-related searches (the distractor lines were surrounded by colored circles matching the prioritized or deprioritized memory color<sup>2</sup>), three distractor-related searches (the distractor lines were surrounded by colored circles matching the prioritized or deprioritized memory color), and six neutral searches (the two memory colors did not reappear in the visual search task). Thus, these twelve possible search arrays were completely agnostic to the colors in the WM array and should not influence WM recall differently for each trial.

For both pre-cue and retro-cue conditions, participants performed three practice blocks to get acquainted with the tasks and then performed 24 experimental blocks, which were divided into two same sessions on two separate days. Participants took part in all three cue reliability conditions in each session. Each cue reliability condition had eight blocks. In the cue conditions with 100% and 50% reliabilities, each block had 12 trials. In the cue condition with 75%

<sup>&</sup>lt;sup>2</sup> The visual searches for prioritized and deprioritized memory colors were analyzed separately. There will always be three target-related searches, three distractor-related searches, and six neutral searches for each memory color within these twelve visual searches.

reliability, half of the blocks had 16 trials, and half had eight trials. This setting was used to ensure cue location and validity were counterbalanced within each block. Each participant completed 288 trials for either the pre- or retro-cue experiment. For both conditions, the total time required for this procedure was approximately two hours.

### Analysis

### WM Task

Our experiment design featured three factors: cue type (two levels: pre-cue vs. retro-cue), cue reliability (three levels: cues with 50% reliability, 75% reliability, and 100% reliability), and cue validity (two levels: valid vs. invalid). However, this design was not fully crossed factorial, since the factor combination of 100% invalid did not exist in the memory task. Therefore, we converted the three-way design to a two-way design with cue type (two levels) as a between-subject factor and cue condition (five levels: 50% valid/invalid, 75% valid/invalid, and 100% valid) as a within-subject factor.

The following data analyses were conducted in R (R Core Team, 2019) using the R packages lme4 (v1.1.21, for linear mixed-effects analyses) (Bates, Maechler, Bolker, & Walker, 2014), afex (v0.23, for linear mixed-effects and ANOVA analyses) (Singmann, Bolker, & Westfall, 2015), and emmeans (v1.3.5, for post-hoc comparisons) unless specifically mentioned. We analyzed memory task accuracy using generalized linear mixed-effects models (GLMMs) with a binomial link function. (G)LMMs have some advantages over the conventional ANOVA approach because they account for individual differences in the model, allowing more of the error to be modeled in addition to fixed factors. It has been suggested that a full random effects structure should be used for significance testing in (G)LMM (Barr, Levy, Scheepers, & Tily, 2013). Thus, to account for participant-level variability, we first constructed the most complex

random-effect structure, including individual intercept and slopes for cue conditions plus their correlations per participant. To assess whether the accuracy results differed between cue types and cue conditions, we included the fixed effects of these two factors and their interaction in the model. However, this full model failed to converge; thus, we simplified the random-effect structure by removing the correlation for random effects, and this parsimonious model could reliably converge.

The significance of fixed effects was assessed with the likelihood ratio test (LRT) using the afex package. The LRT method compares the goodness of fit of the encompassing and reduced models, and it follows asymptotically the  $\chi^2$ -distribution with degrees of freedom equal to the difference in number of parameters between the encompassing and the reduced model (Singmann & Kellen, 2017). To get the main effects of fixed factors, we employed Type III sum of squares and sum-to-zero contrast coding. Post-hoc comparisons of fixed effects and their interactions (if significant) were conducted using z-tests on the estimated marginal means using the emmeans package.

Different from WM accuracy, which followed a binomial distribution and was fitted with GLMM, we ran an LMM to analyze the effects of cue type and cue condition on reaction time. Our analyses were conducted on RTs for correct memory responses only (including all RTs yielded similar results). We used the Satterthwaite's<sup>3</sup> method (Fai & Cornelius, 1996) to evaluate the significance of fixed effects, since it is considered to outperform LRT in unbalanced designs (Kuznetsova, Brockhoff, & Christensen, 2017), which was the case here because our design resulted in a different number of observations for each cue combination condition in the memory task (using the LRT method resulted in similar results). For the post-hoc analysis, we used the

<sup>&</sup>lt;sup>3</sup> We did not use the Satterthwaite method for accuracy, because the GLMMs cannot be estimated with this method.

Satterthwaite's method to estimate the degrees of freedom. Other procedures remained the same as described for fitting the accuracy response.

### **Visual Search Task**

Of primary interest is the pattern of performance on the search task, as this provides a window into how WM representations are being maintained. Toward this end, we investigated the attentional effects for both prioritized and deprioritized colors in the search tasks during the WM delay. We first preprocessed the data by excluding any visual search trials with incorrect responses in the following WM task and removed all RTs to inaccurate search probes. To account for potential counteractive bias effects of the other memory item when both items of the memory array (prioritized and deprioritized colors) were presented on a visual search, we removed search trials that included both memory colors from the WM task in these analyses. For example, when the colors in memory were red and blue, and red was prioritized, the visual searches contained a red prioritized ring with the target inside and a blue deprioritized ring with the distractor inside, or vice versa, were excluded from analysis.

Previous studies (Dowd et al., 2017; Soto et al., 2007) with a 1-item load reported that visual searches were speeded when memory items matched the search targets and were slowed when memory items matched the distractors (relative to neutral searches), which suggested that WM exerts an influence on visual search. To determine whether we replicated both these enhancement and inhibition effects, we carried out a 2 (cue type: pre-cue vs. retro-cue)  $\times$  3 (visual search type: target-related, neutral, distractor-related) ANOVA over the mean RTs with the 100% deterministic cue.

Next, we quantified attentional capture effect<sup>4</sup> for the set of 12 searches on each trial by calculating the difference between the mean RT on target-related visual searches and the mean RT on distractor-related visual searches separately for the prioritized and deprioritized colors. This calculation of attentional capture takes into account both the improvement in memory search from the prioritized/deprioritized color when it matches the target and the slowing of search when it matches a distractor. Attentional capture data were analyzed using linear mixedeffects models with fixed variables of cue type (pre-cue vs. retro-cue), cue reliability (50% reliable, 75% reliable, 100% reliable), memory priority (prioritized vs. deprioritized), and their interactions. Following the same analytic strategy as the memory task, we started by building the maximal random effect model (i.e., cue reliability × memory priority | participant), but this model suffered convergence problems. We, therefore, removed the correlations between random slopes and random intercepts for participants to solve the convergence issue, and further pruned random slope for cue probability and its higher-order interaction with memory priority from random effects structure to overcome the singular fit problem. The simplified model (i.e., memory priority || participant) reliably converged, and when we compared this simplified model with the maximal model with likelihood ratio test, we found no significant difference between these two model fittings (p = 0.85), which suggested that this simplified model was not significantly poorer or better in its fit to the data compared to the maximal model. Thus, we fitted this simplified model using Satterthwaite's method in the following analysis. To break down significant main effects and interactions, we obtained estimated marginal means from the mixedeffects model using the emmeans package, used Satterthwaite's method to estimate degrees of

<sup>&</sup>lt;sup>4</sup> In a separate analysis, we normalized this difference score by dividing the RT differences between target-related and distractor-related visual searches by the mean RT of neutral visual searches (Dowd et al., 2017), the normalization method resulted in similar results as the raw attentional guidance calculation, therefore, the normalization results are not reported here.

freedom of pairwise comparisons, and performed the Holm method to adjust comparisons of factor levels.

We were also interested in whether deprioritized items were dropped from WM based on cue reliability. We determined whether a memory item was actively stored during the memory delay by looking at whether it had influenced the intervening visual searches, which, in turn, resulted in a larger-than-zero attentional capture effect. To achieve this aim, we conducted a series of one-sample t-tests (one-tailed) on six cue conditions (3 cue reliabilities × 2 memory priorities) against zero for pre-cue and retro-cue, respectively. All *P*-values were corrected via the false discovery rate (FDR) method (Benjamini & Hochberg, 1995).

### **Temporal Changes of Attentional Capture Effects**

We hypothesized that different cue reliability and cue type would have different impacts on this temporal change of memory representations, as the decay, no matter it is time-based or interference-based, of representations could be counteracted by guided attention (Ester et al., 2018). However, we were not aiming to quantitatively compare the effects of different cue types and reliabilities on temporal changes of representations, as this would include one more variable (i.e., time) to our already complicated linear mixed model. Instead, we simplified this analysis by exploring different temporal patterns in separate cue conditions.

We divided 12 visual search arrays into six time intervals; each time interval was an average of two adjacent search responses (Q1: searches 1-2, Q2: 3-4, Q3: 5-6, Q4: 7-8, Q5: 9-10, Q6: 11-12). Then we calculated the attentional capture effect for each interval as described above. Attentional capture effects for prioritized and deprioritized WM items and different quartiles were assessed using a two-way repeated-measures ANOVAs with factors of memory priority (prioritized vs. deprioritized) and time interval (from Q1 to Q6), separately for each cue

type and cue reliability condition. The p values were adjusted for sphericity violations using the Greenhouse-Geisser correction to the degrees of freedom when necessary. Once we observed a significant main effect of interval or interaction between interval and priority, we conducted a polynomial trend analysis to examine which trends fitted the interval results better.

### **Relationships between Attentional Capture Effects and Memory Performance**

To investigate the relationship between the strength of memory representations during the delay and the final memory recall performance, we built either LMM or GLMM depends on whether the dependent variable was accuracy outcome (i.e., 0 or 1) or RT. The Satterthwaite's method and the LRT method were used separately for LMM and GLMM to evaluate the significance of fixed effects. The prioritized and deprioritized attentional captures were included as fixed variables, and individual intercept per participant as the random variable. Different from WM task RT analysis, which only used RTs on correct trials, in this analysis, RTs on both correct and incorrect memory trials were included. We collapsed data of each trial across cue type and cue reliability, because if the memory strength during the delay could predict retrieval performance, then it should be independent of cue manipulations.

#### **CHAPTER 3**

### RESULTS

We excluded participants with poor memory and visual search accuracy separately for the pre-cue and the retro-cue group using their respective median performance scores (Leys, Ley, Klein, Bernard, & Licata, 2013). In the pre-cue group, three participants were excluded because of their poor memory performance (> 3 median absolute deviations (MAD) from the median (93.40%) across all participants), and one participant was further excluded because that person's overall visual search accuracy was below 3 MAD of the median (95.62%) of the remaining participants (32 participants). With the same exclusion criteria, in the retro-cue group, we excluded four participants who had poor memory accuracy (median accuracy of all participants: 90.62%), and no remaining participants: 94.01%). Thus, four participants were excluded in each group, leaving 31 participants in the pre-cue group and 31 participants in the retro-cue group.

#### WM Task Performance

# Accuracy

Overall median accuracy was 94.10% (M = 92.85%, SD = 4.87%) in the pre-cue group, and 91.32% (M = 88.59%, SD = 7.63%) in the retro-cue group. To investigate how the cue type and cue condition affected memory accuracy and RT, we constructed mixed-effects models to examine their main effects and interaction.

The overall 2 (cue type: pre-cue vs. retro-cue) × 5 (cue condition: 50% valid, 50% invalid, 75% valid, 75% invalid, and 100% valid) GLMM on memory accuracy revealed a significant main effect of cue type with  $\chi^2$  (1) = 5.91, *p* = 0.02. Consistent with previous studies

(Myers et al., 2015; Robison & Unsworth, 2017; Souza, 2016), the pre-cue group had significantly better performance than the retro-cue group. We also observed a significant main effect of cue condition,  $\chi^2$  (4) = 24.05, p < 0.001. Post-hoc contrasts with Holm correction (Holm, 1979) revealed that probe colors at prioritized locations had higher accuracy than at deprioritized locations when the cue was 75% reliable (valid vs. invalid, z = 4.65, p < 0.0001), however, this comparison was not significant when the cue was not predictive (valid vs. invalid, z = 0.63, p = 0.76).

When we compared the effects of cue reliability for only valid trials, we found higher accuracy in the 100% reliable condition than the two other conditions (75% vs. 100%, z = -3.04, p = 0.01; 50% vs. 100%, z = -3.61, p = 0.002). However, the difference between the 50% and 75% reliability cues was not significant (50% vs. 75%, z = -0.87, p = 0.76). On invalid trials, accuracy was higher in the 50% reliable than the 75% reliable condition (z = 3.01, p = 0.01). The interaction between cue type and cue condition, however, was not reliable ( $\chi^2$  (4) = 8.41, p = 0.08) (Figure 2A), suggesting that the effect of cue reliability was equivalent for pre-cues and retro-cues.

Our results suggested that the cueing costs varying with cue reliability may not be tightly associated with the cueing benefit changes, as there was a performance difference between the 50% and 75% reliable cues for invalid trials, but not a difference for valid trials. Furthermore, we compared the magnitudes of validity effect (valid-invalid accuracy) between 50% and 75% reliable cue conditions using a mixed-design ANOVA with cue type (pre-cue vs. retro-cue) as the between-subject variable and cue reliability (50% reliable vs. 75% reliable) as the within-subject variable. The results suggested that the main effect of cue reliability was significant (F(1,60) = 7.60, p = 0.008,  $\eta_p^2 = 0.11$ ), and the 75% reliable cue resulted in greater validity

effect than the 50% reliable cue. This greater cueing effect was due to worse performance in invalid trials in the 75% cue condition (z = 3.01, p = 0.01) rather than better performance in valid trials (50% vs. 75%, z = -0.87, p = 0.76). The main effect of cue type and the interaction effect between cue type and cue reliability were not significant (both *Ps* > 0.1).

### RTs

When we conducted analyses on RTs, we only analyzed trials with correct memory responses. Results of the LMM for RTs showed a significant main effect of cue condition (F(4,111.86) = 56.70, p < 0.001), however, neither the main effect of cue type, F(1,59.94) = 0.28, p = 0.60, nor the interaction between cue type and cue condition was significant, F(4, 111.86) = 0.40, p = 0.81. Similar to the results for accuracy, post-hoc comparisons of cue condition suggested that the RTs for valid trials were faster than invalid trials in the 75% condition (valid vs. invalid, t(143.8) = -4.06, p = 0.004), but not in 50% condition (valid vs. invalid, t(149.7) = -2.25, p = 0.09).

When the comparisons were focused on valid trials only, RT was fastest in the cue condition with 100% reliability compared to both 75% and 50% reliable conditions (100% vs. 75%, t(93.6) = -12.52, p < 0.001; 100% vs. 50%, t(114.8) = -13.90, p < 0.001), but again, the RT difference between the latter two conditions was not significant (t(149.8) = 0.17, p = 0.86). There was no significant RT difference between the two invalid conditions (50% vs. 75%, t(184.7) = -1.90, p = 0.12) (Figure 2B). All p-values were corrected using the Holm method.



**Figure 2. Memory performance in the pre-cue and retro-cue task.** (A) Memory accuracy for factors cue type, and cue combination condition. Raw individual accuracies (in points) and their averages (in bars) for each condition were displayed. Error bars represent 95% within-subject confidence interval. Note, we showed raw percentage values to allow a comparison to previous studies, whereas, for statistical analysis, a log-linked GLMM was applied to single-trial accuracy values (i.e., 0 or 1). (B) Response time for different cue combination conditions. Data were collapsed over the pre-cue and the retro-cue conditions, as this manipulation did not render significant results (see main text for details). In this graph, the estimated marginal means (hollow circles) and within-subject error bars (represent 95% confidence interval) were plotted in the foreground, and the raw data (half boxplot and half semitransparent individual points) were plotted in the background.

Similarly, we conducted a mixed-design ANOVA with cue type and cue reliability on RT to investigate whether the 75% reliable cue would result in greater validity effect than the 50% reliable cue as in the accuracy results. Again, the results suggested that the 75% reliable cue

resulted in greater validity effect (invalid-valid RT) than the 50% reliable cue (F(1,60) = 5.82, p = 0.02,  $\eta_p^2 = 0.09$ ), and this greater effect was driven by the RT differences in invalid trials. The main effect of cue type and the interaction effect between cue type and cue reliability on RT were not significant (both *Ps* > 0.1).

### **Interim Summary**

This design successfully replicated many previous results (for a summary of the results, see Table 1) and supported most of our hypotheses. First, better performance was observed for pre-cues compared to retro-cues in accuracy (Robison & Unsworth, 2017; Souza, 2016). Second, participants strategically used the cue to guide attentional selection, as the performances were equivalent for valid and invalid trials in 50% reliable cue condition, and better for valid trials than invalid trials in 75% reliable cue condition. Third, participants used the cue to adjust their prioritization based on cue reliability. Memory performance was much better for the deterministic cue than probabilistic cues, but the comparable performances of 50% and 75% reliable cue reliability. However, the hypothesis that directing attention externally or internally would influence the utilization of cueing information was not supported, as there was no interaction between cue type and cue condition on either accuracy or RT.

# Table 1.

Summary of WM task results.

	Results				
Measures		Interaction			
-	Cue Type Cue Condition				
		Valid vs. Invalid			
	-	50%	No difference		
		75%	valid > invalid		
	-	Valid Only		_	
ACC	Pre-cue > Retro-cue	50% vs. 75%	No difference	Null	
		75% vs. 100%	100% > 75%		
		50% vs. 100%	100% > 50%		
		Invalid Only		_	
	-	50% vs. 75%	50% > 75%		
		Valid vs. Invalid			
	-	50%	No difference	_	
		75%	valid < invalid		
	-	Valid Only			
RT	No difference	50% vs. 75%	No difference	Null	
		75% vs. 100%	100% < 75%		
		50% vs. 100%	100% < 50%		
	-	Invalid Only			
	-	50% vs. 75%	No difference		

### **Visual Search Task Performance**

In this part of analysis, we mainly examined how cue type and cue reliability affect WM representations during maintenance. First, to demonstrate that our design resulted in memory-based attentional bias, we conducted a 2 (cue type: pre-cue vs. retro-cue) × 3 (visual search type<sup>5</sup>: target-related, distractor-related, neutral) mixed ANOVA with a Greenhouse-Geisser correction over the individual mean visual search RTs on data with 100% reliable cues. Specifically, in this deterministic cue condition, within individuals, we averaged all RTs of target- and distractor-related and neutral visual searches separately, for the prioritized memory items. We expected to find that the target-related visual searches resulted in the fastest responses, followed by the neutral searches, and the distractor-related searches had the slowest responses.

The ANOVA results revealed that there was no significant main effect of cue types  $(F(1,60) = 0.04, p = 0.85, \eta_p^2 = 0.001)$ ; as expected, there was a significant main effect of visual search type  $(F(2,120) = 27.12, p < 0.001, \eta_p^2 = 0.31)$ . The interaction between cue type and visual search type was not significant  $(F(2,120) = 1.94, p = 0.16, \eta_p^2 = 0.03)$ . Bonferroni corrected post-hoc t-tests showed that participants responded faster on target-related visual searches (M = 221.90 ms, SD = 38.17 ms), t(61) = -2.41, p = 0.06, although unreliably, and slower on distractor-related visual searches <math>(M = 223.86 ms, SD = 37.52 ms) (Figure 3). Even though these results did not entirely replicate the target-related attentional bias, it still suggested that WM could bias attention towards visual searches sharing the same feature. Therefore, it should not undermine our approach of using the difference between target- and distractor-related

<sup>&</sup>lt;sup>5</sup> Both prioritized and deprioritized memory colors in each memory trial had their corresponding visual searches. Here, this confirmation analysis was focused on visual search RTs for prioritized memory color only.

attentional bias to represent the strength of memory representation. The marginal effect of targetrelated attentional bias might be related to the verbalization of the visual stimulus, and we discussed more about this in the general discussion.



**Figure 3. Mean search response times by visual search types.** The response time was faster on target-related searches and slower on distractor-related searches, compared to neutral searches. The *p* values reported here were Bonferroni corrected. This data was collapsed across pre- and retro-cue conditions.

#### **Attentional Capture Effects**

Next, we analyzed how different cue reliabilities and cue types would affect the attentional capture effect. Only data with correct visual searches (pre-cue: M = 95.22%, SD = 2.65%; retro-cue: M = 93.18%, SD = 2.91%) were included in this attentional capture analysis. We fitted a linear mixed model that included three experimental factors, that is, cue reliability, memory priority, and cue type. It is worthwhile to mention that memory priority depended on whether an item was prioritized but not whether it was probed. This is because attentional capture effects of

memory priority, F(1,53.63) = 10.69, p = 0.002, and cue reliability were observed, F(2,32076.25) = 4.63, p = 0.01, indicating that prioritized colors induced stronger attentional capture than deprioritized colors and that the attentional effect increased with cue reliability. The only significant interaction observed was between cue type and cue reliability, F(2,32076.25) = 6.05, p = 0.002. The three-way interaction between cue reliability, memory priority, and cue type was not significant, F(2,32085.52) = 0.94, p = 0.39, reflecting that the interactions between cue reliability and memory priority were not significantly different in the pre-cue and retro-cue conditions (Table 2).

To break down the cue type × cue reliability interaction effect, we first investigated the effect of cue type on attentional capture for each cue reliability condition. After controlling for family-wise error rate using the Holm method, our results suggested that 100% deterministic retro-cues resulted in significantly greater attentional capture than pre-cues, t(275) = 2.77, p = 0.02; however, there were no differences between pre- and retro-cues in other cue reliability conditions (Figure 4). We then examined how attentional capture changed with cue reliabilities for each cue type. Our results indicated that retro-cue reliability could modulate attentional capture, as suggested by the stronger attentional capture effect in the cue condition with 100% reliability (t(32102) = 4.40, p < 0.001). However, the difference between cue conditions with 75% and 50% reliabilities was not significant (t(32073) = 1.76, p = 0.32). Surprisingly, when the pre-cue was implemented, the effect of attentional capture did not change with cue reliabilities (p > 0.1 in all three comparisons).

### Table 2.

Predictor	Numerator DF	<b>Denominator DF</b>	F	Р
Cue Reliability	2	32076.25	4.63	0.01
<b>Memory Priority</b>	1	53.63	10.69	0.002
Cue Type	1	58.63	0.10	0.75
Cue Reliability × Memory Priority	2	32085.52	1.65	0.19
Cue Reliability × Cue Type	2	32076.25	6.05	0.002
Memory Priority × Cue Type	1	53.63	1.13	0.29
Cue Reliability × Memory Priority ×	2	32085.52	0.94	0.39
Cue Type				

### Results of LMM for attentional capture effects.

Note. The degree of freedoms and p values were obtained with the Satterthwaite approximation. Bolded values indicated significance at p < 0.05. DF = degree of freedom.

### **Interim Summary**

The LMM on attentional capture and their post-hoc analyses only partially supported our hypotheses. First, prioritized items overall induced higher attentional capture than deprioritized items. Second, different cue types could also affect attentional capture; however, different from their effects on the memory retrieval performance, the effect of cue type on memory-driven attentional capture was modulated by cue reliability. The interaction of cue type and reliability suggested that attentional capture increased with cue reliability in the retro-cue condition but not in the pre-cue condition. The effect of retro-cue was to increase attentional capture of both prioritized items suggesting that the reliability strengthened representations of both items. Third, we did not find evidence that cue reliability was used to effectively allocate

more attentional resources to prioritized than deprioritized items either for internal or external attention, as there was no two-way interaction between cue reliability and memory priority, and no three-way interaction among cue reliability, memory priority, and cue type.



confidence interval) were plotted in the foreground, and the raw data (half boxplot and half semitransparent individual points) were plotted in the background. Significant comparisons were marked with asterisk. \* p < 0.05; \*\*\* p < 0.001.

### **Status of Memory Representations**

In Chapter 1, we mentioned that the magnitude of attentional capture could reflect the status of mental representations, and we hypothesized that if one item had close-to-zero attentional capture, it might suggest that the mental representation of that item was not kept in memory, at least at that moment. Our abovementioned results have suggested that prioritized

WM items generally had greater representation strength than deprioritized items; however, we still did not know their respective fates under different cue reliability conditions. To probe the states of both prioritized and deprioritized items, we conducted one-tailed one-sample t-tests against zero to investigate whether individual memory items under different cue reliability conditions were actively stored (i.e., larger-than-zero) or not (i.e., equals to zero) during WM maintenance in either pre- or retro-cue condition. *P* values were corrected with the FDR approach (Table 3).

Among these tests, when the cue was 100% reliable, prioritized memory items had significantly larger-than-zero attentional capture in both pre-cue (mean = 6.02 ms, t(30) = 3.71, p = 0.001) and retro-cue conditions (mean = 10.62 ms, t(30) = 5.18, p < 0.001) (Figure 5); the attentional capture effects of deprioritized memory items were not significantly different from zero in the pre-cue condition (mean = 0.11, t(30) = 0.08, p = 0.47), but different from zero in the retro-cue condition (mean = 5.74 ms, t(30) = 3.02, p = 0.01). The result in the pre-cue condition was consistent with the removal account, that is, the irrelevant item was expelled from memory storage. However, the irrelevant item in the retro-cue condition with 100% reliability was preserved in memory, suggesting that the retro-cue might not be able to properly allocate memory resources to items in proportional to their testing probabilities.

## Table 3.

Summary of one-tailed one-samp	ole t-tests by conditions.
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				t-tests		
		-	M	t	df	р
	500/	Prioritized	2.57	1.73	30	0.06
	5078	Deprioritized	4.22	2.24	30	0.02
- Dra qua	75%	Prioritized	6.33	4.01	30	0.001
Pre-cue	7370	Deprioritized	3.25	2.35	30	0.025
_	100%	Prioritized	6.02	3.71	30	0.001
		Deprioritized	0.11	0.08	30	0.47
	50%	Prioritized	2.72	1.22	30	0.17
	5070	Deprioritized	-1.54	-0.86	30	0.80
- Retro-cue	-cue 75%	Prioritized	6.57	2.16	30	0.04
Keno-eue		Deprioritized	1.37	0.74	30	0.28
-	100%	Prioritized	10.62	5.18	30	0.00004
	10070	Deprioritized	5.74	3.02	30	0.01

Note. *P* values are FDR-adjusted for pre- and retro-cue conditions separately. Bolded values indicate significance at p < 0.05, and italicized values indicate a trend towards significance at p < 0.1. M = mean, units are milliseconds.

When the cue was predictive but not deterministic (i.e., 75% reliable), in the pre-cue condition, both the prioritized items (mean = 6.33 ms, t(30) = 4.01, p = 0.001) and deprioritized items resulted in significant larger-than-zero attentional capture effects (mean = 3.25 ms, t(30) = 2.35, p = 0.02). However, when the retro-cue was implemented, only the prioritized item (mean

= 6.57 ms, t(30) = 2.16, p = 0.04), but not the deprioritized item (mean = 1.37 ms, t(30) = 0.74, p = 0.28), had larger-than-zero attentional capture effects.

Lastly, when the cue was nonpredictive (i.e., 50% reliable), the deprioritized item in the pre-cue condition exhibited a larger-than-zero attentional effect (mean = 4.22 ms, t(30) = 2.24, p = 0.02), while the attentional effect for the prioritized item only showed a marginal trend toward significance (mean = 2.57 ms, t(30) = 1.73, p = 0.06). The effects of attentional capture in the nonpredictive retro-cue conditions were not significantly different from zero (p > 0.1).



Figure 5. Attentional capture effects for factors cue type, cue reliability, and memory priority. The left panel represented the pre-cue condition, and the right panel represented the retro-cue condition. Prioritized and deprioritized conditions were indicated in different colors. The estimated marginal means (colored circles) from the LMM and within-subject error bars (represent 95% confidence interval, in bold lines) were plotted in the foreground, and the raw data (half boxplot and half semitransparent individual points) were plotted in the background. One-tailed one-sample t-test results were displayed. \* p < 0.5; \*\*  $p \le 0.01$ ; \*\*\*  $p \le 0.001$ . *P* values were FDR-corrected for multiple comparisons separately for pre- and retro-cue conditions.

### **Interim Summary**

In addition to comparing the magnitudes of attentional capture on different experimental conditions, we compared the attentional capture to zero to explore the fates of memory representations qualitatively during the memory delay. The fates of memory representations were mostly consistent with our predictions when the attention was externally guided: (1) the deprioritized memory item was expelled from active memory storage during the delay when the cue was 100% reliable; (2) when the cue was probabilistic, both prioritized and deprioritized memory items were preserved, even though the evidence for the prioritized item in 50% reliable cue condition was not very reliable. However, the fates of memory representations were mostly inconsistent with our predictions when the attention was internally guided: (1) when the retrocue was 100% reliable, even though the deprioritized item was unlikely to be probed, it was still stored during the delay; (2) when the retro-cue was 50% reliable, even though both memory items were likely to be probed, they were not stored during the delay as the results suggested. We will discuss these puzzling results more in general discussion.

#### **Temporal Changes of Memory Representations**

In this part of analysis, we examined how attentional capture effects changed with time during memory delay for each cue condition separately (Figure 6). When the cue was deterministic (i.e., 100% reliable) and attention was directed externally, a two-way repeated-measure of ANOVA with factors of memory priority (prioritized vs. deprioritized) and time interval (from Q1 to Q6) revealed that prioritized items overall had significantly larger attentional capture effects than deprioritized items (F(1,30) = 9.32, p = 0.005), but there were no main effect of interval (F(4,124) = 1.37, p = 0.25) or interaction between memory priority and interval (F(4, 134) = 2.05, p = 0.08). These results suggested that both memory representations

were maintained in a constant pattern during the delay, even though their strengths were different. When attention was directed internally, there was a main effect of time interval (F(4,115) = 3.32, p = 0.01), but other effects were not significant (both p > 0.1). The following polynomial trend analysis revealed that there was a significant negative linear trend ( $\beta = -56.78$ , t = -2.40, p = 0.02) and a positive quadratic trend ( $\beta = 70.03$ , t = 2.71, p = 0.008). Thus, attentional capture effects decreased with time overall, though there was a bounce-back in the middle, possibly starting from the fourth interval (Figure 6). These results suggested that even though there were some fluctuations during the maintenance of memory representations, probably due to the internal attention strength is not as strong as external attention, both memory items remained in an elevated state.

When the pre-cue was predictive (i.e., 75% reliable), similar to deterministic pre-cue condition, prioritized items resulted in larger, although unreliably, attentional capture effects than deprioritized items, F(1,30) = 3.71, p = 0.06, no main effect of time interval or interaction effect were observed (both p > 0.1). However, in the retro-cue condition with a predictive cue, both main effects of memory priority and time interval and their interaction were not significant (all p > 0.1). Together, these results suggested that when a predictive cue was given, no matter attention was directed externally or internally, both memory representations remained consistent despite their status (see Table 3).

Lastly, when the pre-cue was nonpredictive (i.e., 50% reliable), we observed a significant main effect of time interval (F(4,120) = 2.96, p = 0.02), and a significant interaction between time interval and memory priority (F(4,134) = 2.32, p = 0.05), no difference between prioritized and deprioritized items was observed (F(1,30) = 0.85, p = 0.36). The polynomial trend analysis indicated that for prioritized memory representation, there was a negative linear trend ( $\beta = -$ 

67.80, t = -1.98, p = 0.05) and a negative cubic trend ( $\beta = -135.52$ , t = -2.47, p = 0.01). For deprioritized memory representation, there was a negative quartic trend ( $\beta = -50.06$ , t = -2.31, p = 0.02). These results suggested that both memory representations were volatile during the memory delay, which was different from our hypothesis that representation strengths decrease with time when attention is not guided to either of memory items. There were no significant effects of memory priority, interval, and their interaction on attentional capture (all p > 0.1) when a nonpredictive retro-cue was implemented.

### **Interim Summary**

Overall, our empirical results failed to support our hypotheses. Across different cue conditions, we mainly observed constant attentional capture effects over time intervals, as suggested by the null effects of the time interval. However, the null effects might have different meanings in different cue conditions. If the memory colors were actively stored, as suggested by previous memory representation status analysis, the null results might suggest they remained elevated during the delay. However, if they were not actively stored, that might suggest the loss of memory information was not reversed during the delay, and unfortunately, our method failed to capture the information loss process. For example, in the pre-cue condition with 100% reliability, there were no main effect of interval and no interaction effect. According to previous results (Table 3), the prioritized memory color was preserved in this condition, while the deprioritized memory color was purged. Therefore, the prioritized color might remain elevated during time intervals; however, the deprioritized color might remain removed from memory, at least in the observed time window. This behavioral result did not exclude the possibility that the representation of deprioritized color degraded rapidly in the initial time window; our method might not have a high temporal resolution to capture this rapid change.


Priority - Prioritized - Deprioritized

**Figure 6.** Attentional capture effect of time interval in different cue conditions. RT differences between targetand distractor-related visual search probes in the 12-trial visual search set were separated into six intervals. Points and error bars represented means and within-subject 95% confidence intervals.

#### **Relationships between Memory Representations and WM Performances**

The different effects of manipulated cue factors on retrieval performance and on the strength of mental representations seemed to suggest that there is no one-to-one mapping between these two measures. Additionally, one-sample t-test results suggested that some cue conditions, especially the nonpredictive retro-cue condition, had close-to-zero attentional capture effects. However, their memory performances were still quite accurate. For example, both

averaged memory accuracies for valid and invalid trials in the nonpredictive retro-cue condition were above 80%. Consequently, one might be wondering whether the precision of mental representation, as indicated by the magnitude of the attentional capture effect, is dissociated (partially or wholly) with the final memory performance. We investigated this question by conducting LMM and GLMM to explore the relationships between the strength of memory representation during the delay and final retrieval RT and accuracy outcome.

Consistent with our observations, neither prioritized ( $\chi^2$  (1) = 0.71, p = 0.40) nor deprioritized ( $\chi^2$  (1) = 0.33, p = 0.57) memory representation could predict memory accuracy. Similarly, retrieval RTs could not be predicted by either prioritized (F(1, 17529.57) = 0.73, p = 0.39) or deprioritized (F(1, 17528.54) = 0.57, p = 0.45) memory representation. Therefore, these results suggested that the strength of WM representations during maintenance could not predict upcoming memory recall performance.

#### **CHAPTER 4**

# **GENERAL DISCUSSION**

How does the effect of directing attention externally via a pre-cue on WM differ from directing attention internally via a retro-cue? How would presenting spatial cues with different reliabilities impact memory performance and change the status of mental representations of WM? What are the fates of prioritized and deprioritized items during memory maintenance, and how would they change with time? What are the relationships between the status of memory representations during maintenance and the final memory retrieval performance? There are many unanswered questions regarding the storage and retrieval of relevant and irrelevant information in WM.

To answer these questions, we implemented different cue reliabilities and cue types in a dual task, then tested whether these factors impact the WM task at retrieval and the intervening visual search task during the delay. Because we measured a series of visual search responses in each memory task trial, we could explore how the strengths of memory representations changed over time course. Last, we investigate how the strength of memory representations accounts for final memory retrieval performance. In brief, we found that different cue types and cue reliabilities could affect both final memory retrieval performance and the internal status of memory representations during the delay, but in a different way. Further mixed model analyses confirmed our observation that the strength of memory representations could not predict final memory retrieval performance. In many cue conditions, the strengths of memory representation remained constant across the delay, regardless of whether attention was guided to or not.

The experiments presented in this dissertation were based on Mallett and Lewis-Peacock's (2018) work, which demonstrated that both the mental representations of prioritized

and deprioritized colors in a memory trial could be behaviorally decodable during memory maintenance. Importantly, they suggested that the attentional capture effect in visual search induced by remembered memory content could be a proxy for the strength of the memory representation. The authors used a behavioral paradigm which was previously used in neuroimaging decoding studies (LaRocque et al., 2013; Lewis-Peacock et al., 2012), and found similar results regarding the status of mental representations which previously were only observed with neuroimaging methods. Here, we extended their paradigm by including different cue types and cue reliabilities to investigate how attentional demands flexibly control WM representations. It is well established that participants use search templates or attentional templates maintained in visual WM to guide visual search task (Carlisle, Arita, Pardo, & Woodman, 2011; Desimone & Duncan, 1995). In the present study, we considered the search template as equivalent to a WM representation from the memory recall task. However, one might question whether they are essentially the same. In one recent study, researchers (Gunseli, Meeter, & Olivers, 2014) compared the ERP components for maintaining a visual WM representation during a simple recognition task, which did not involve the visual search, and two search tasks with different difficulties. Their results suggested that search templates are qualitatively the same as visual WM representations used in the recognition task in terms of ERP components. Therefore, the magnitude of the memory-related capture effect, which represents the strength of the search template, could also reliably represent the strength of the WM representation. It is worthwhile to mention that our expression of memory representation strength is different from previous studies using the final memory outcomes, whether they were binary or continuous, as a measure of memory representation.

## The Effects of Cue Type and Cue Reliability on WM

The current study suggests that both cue type and cue reliability can regulate memory recall performance and the strength of memory representations. In line with previous findings (Myers et al., 2015; Robison & Unsworth, 2017; Souza, 2016; Souza, Thalmann, & Oberauer, 2018; Thibault, van den Berg, Cavanagh, & Sergent, 2016), we found pre-cues are more effective than retro-cues at improving memory retrieval performance, as suggested by the higher retrieval accuracy in the pre-cue condition.

It has been proposed that both the fluctuations in bottom-up stimulus properties and viewing conditions during encoding (Wildegger, Humphreys, & Nobre, 2016) and intrinsic noise fluctuations (Fougnie, Suchow, & Alvarez, 2012; van den Berg et al., 2012) can impact the stability of WM representations and final retrieval performance. Guiding attention either before or after the memory array might help to counteract external or internal variabilities that are detrimental to memory performance. The cueing advantage of external attention relative to the internal attention might be related to its ability of enhancing precisions of memory items at retrieval, rather than enhancing the probabilities of memory items available for retrieval (Wallis et al., 2015). In line with this argument, a recent study (van Ede, Chekroud, Stokes, & Nobre, 2018) combined stimulus orientation decoding and EEG to investigate how anticipation, implementing an auditory pre-cue, influences the sensory information processing of target orientation when facing a competing distractor. Their results suggested that anticipatory states not only enhance neuronal target representations but also provide a protected temporal window for the target from interference caused by distractors. Therefore, the pre-cue can affect the representation qualities of target stimuli, probably through protecting them from interferences of competing distractors.

Previous fMRI work also found different spatial patterns of cortical recruitment between pre- and retro-cues. For example, Wallis et al. (2015) performed meta-analyses for pre-cue and retro-cue fMRI studies. They found that pre-cues and retro-cues both activated the frontoparietal network, while retro-cues additionally activated the cingulo-opercular network. The frontoparietal network is hypothesized to be responsible for mediating top-down control over the sensory cortex, whether this is to focus sensory processing only on the relevant information at the early preparation stage or to control the focus of attention among items being maintained in WM (Gazzaley & Nobre, 2012). Complementing this hypothesis, studies have demonstrated that functional connectivity between the prefrontal cortex and visual areas during WM encoding (Zanto, Rubens, Thangavel, & Gazzaley, 2011) and maintenance (Kuo, Yeh, Chen, & D'Esposito, 2011) was causally related to subsequent WM performance. Following retro-cues, the cingulo-opercular network could also be engaged, and it was previously hypothesized to maintain task set over longer periods. However, Wallis et al. (2015) found that the cinguloopercular network was transiently recruited following retro-cues, suggesting that it was not directly involved in control over sensory representations, but perhaps specifically associated with output gating.

Our memory retrieval performance results suggested that participants could allocate attentional resources along with task demands, with cueing benefits stemming from different mechanisms depending on the reliability of cues. As expected, in both the pre- and retro-cue conditions, the deterministic cue with 100% reliability resulted in the highest memory performance (in both accuracy and RT), and the deprioritized items in predictive cue conditions, which only had a 25% of chance of being probed, had the worst recall performances (though only significant in accuracy). However, the memory performance did not linearly change with

cue reliabilities, even though the 100% reliable cue would benefit the prioritized memory item more than the 75% reliable cue, the 75% reliable cue and 50% reliable cue resulted in equivalent performance, in both accuracy and RT, for prioritized items. This result demonstrated that observers could not (or preferred not to) allocate their memory resources precisely in line with the cue reliabilities.

We suspect that participants in our study treated the prioritized items in predictive and nonpredictive cue conditions the same. Since they experienced all three cue reliability conditions in the experiment, the reliability contrast for prioritized items between the predictive and nonpredictive cue conditions might not be as striking as the contrasts between deterministic cue and other two cue conditions. In the deterministic cue condition, participants knew they could completely trust the cue; however, in the predictive cue condition, they probably only had a vague idea that the prioritized item was slightly more likely to be probed, and their perceived reliabilities might differ from the actual reliability. However, that does not imply that the predictive cue condition has no advantage compared to the nonpredictive cue condition. When the combination of prioritized benefit and deprioritized cost was considered, predictive cues still resulted in a greater cueing effect than nonpredictive cues, as suggested by the greater performance difference between valid and invalid trials in the 75% reliable cue condition than in the 50% reliable cue condition.

Even though our results revealed that participants performed better when they knew the cue was 100% reliable than when the cue was only 75% reliable, not all studies had the same conclusion. For example, in one previously described study, Dube et al. (2019) found there was no memory recall difference for the prioritized item when the cue was 70% versus 100% reliable. Different from our design of using a limited number of memory colors, their task sampled two

memory colors randomly from a 360° color wheel and asked participants to determine whether the probe color was 30° off from the target color on the color wheel. Therefore, their task was more difficult than our task; in this case, in order to perform well, participants perhaps had to put an equivalent amount of effort into both cue conditions. This discrepancy might indicate that task difficulty could modulate the effects of cue reliability on final WM performance. Future work might want to investigate how participants utilize cue information facing different task difficulty.

Some decoding literatures has investigated how mental representations changed during memory delay with or without the presence of an informative cue (Ester et al., 2018; Nouri & Ester, 2019), and others investigated how switching the priority between memory targets would transform the status of different representations (LaRocque et al., 2014; Lewis-Peacock et al., 2012; Mallett & Lewis-Peacock, 2018; Wolff et al., 2017). However, to the best of our knowledge, no study has directly compared the quantitative changes in mental representations as a function of attentional demand directed by cue reliability. Thus, the primary purpose of this study is to fill this research gap.

Our results suggested that the strengths of WM representations during WM maintenance, assessed by the magnitude of memory-driven attentional capture, are modulated by cue reliabilities as well. However, unlike the WM retrieval performance showed no interaction between cue reliability and cue type, modulation effects of cue reliability on memory representations differed for pre- and retro-cue. The effects of retro-cue reliability on memory representations resembled their effects on memory retrieval performance when memory priority was ignored (as only the interaction between cue type and cue reliability was significant), such that the deterministic cue resulted in the strongest memory representation, and predictive and nonpredictive cues resulted in comparable strength of memory representations.

It seemed the pre-cue reliability did not affect memory representations, as the attentional capture effects did not change with cue reliabilities when the memory priority was ignored. However, the attentional effect might be hidden by the memory priority. In an exploratory analysis (not listed in the Results section), as we broke down the attentional capture effects for the pre-cue and retro-cue groups separately, we found there was an interaction between cue reliability and memory priority in the pre-cue condition. This interaction might contribute to the null effect of cue reliability reported in the pre-cue condition, while there was no interaction between cue reliability and memory priority in the retro-cue condition. Together, these results suggested that internal attention might only be sensitive to varying cue reliabilities, but not be effective at prioritizing information within one cue reliability condition; therefore, we found both prioritized and deprioritized memory representations were enhanced with cue reliability. In contrast, external attention might be better at both relative to internal attention; therefore, we observed the memory representation strengths for prioritized/deprioritized items increased/decreased with cue reliabilities in the pre-cue condition. However, we must interpret these results with caution, as the three-way interaction among cue reliability, memory priority, and cue type was not significant.

Given the close relationship between mental representation and final memory retrieval, it is natural to presume that the precision of mental representations might be correlated with memory performance during recall. Neuroimaging evidence has shown that the precision of neural representation during the delay period was related to behavioral performance on memory recall task (Ester, Anderson, Serences, & Awh, 2013; Wolff et al., 2017). For example, Wolff et al. (2017) found that decoding information for prioritized memory presentation with a 100% reliable retro-cue was related to the memory item's precision, acquired from the mixture model,

but not the guess rate. Neither the memory precision nor the guess rate was related to decoding information for the deprioritized memory representation. However, our results were not consistent with this neuroimaging result. We found neither prioritized nor deprioritized attentional capture effect could predict final memory performances.

A recent behavioral study (Hollingworth & Hwang, 2013) reported similar results as ours. The authors implemented an 80% reliable retro-cue to investigate the relationship between memory recall performance for deprioritized items and the visual search RT impacted by the deprioritized memory item. The hypothesis was that memory performance should have increased as the search RT increased. However, their results suggested there was no relationship between the precision, calculated from the mixture model, of the memory item, and the degree of attentional capture induced by the memory item. The underlying mechanisms causing the discrepancies between neuroimaging and behavioral measures of memory representations are largely unknown. One potential explanation could be that even though both measures can represent parts of the actual memory information, they do not measure the same. Future researchers may want to combine this behavioral measure and neuroimaging decoding analysis to investigate the possibilities.

## The Fates of Prioritized and Deprioritized WM Representations

The fates of prioritized and deprioritized items could rely on cue reliabilities and cue types. In the pre-cue condition, when memory items had a chance to be probed (i.e., probe probability is larger than zero), the magnitudes of attentional capture effects were above the baseline (i.e., the magnitude equals to zero). Prioritized items had more substantial attentional capture effects than deprioritized items in both deterministic and predictive cue conditions, but not in nonpredictive cue condition. However, in the retro-cue condition, the pattern was not that

clear: (1) the deprioritized item in the deterministic cue condition was not expelled from memory storage as expected, and we found no significant differences between attentional effects of the prioritized and deprioritized items (see polynomial trend analysis); (2) the prioritized item in the predictive cue condition showed a detectable attentional capture effect, but not the deprioritized item, and their difference was not significant; (3) neither the prioritized nor deprioritized items in the nonpredictive cue condition captured attention and interfered with visual search during memory delay.

Attending to what is relevant and ignoring what is irrelevant is vital for the effective utilization of limited WM resources. Several studies confirmed that an item deprioritized for retention by a retro-cue in VWM would be suppressed and, therefore, no longer affect visual search (Olivers et al., 2006), even when the cue was not deterministic (e.g., 80% reliable, Hollingworth & Hwang, 2013). However, our attentional capture effect results for deprioritized WM items in the deterministic retro-cue condition suggested that suppression might not always be successful, even when the memory item is completely task-irrelevant. There were two possible explanations on this incomplete memory removal: (1) the deprioritized WM content might remain in a fragile state even though they are never required for further performance (Schneider, Mertes, & Wascher, 2015); (2) the retro-cue could not effectively divert attention away from internal representations once encoded such that attention could be spilled over into the deprioritized item.

According to the first explanation, deprioritized items are no longer held activated in WM, yet this status does not exclude their ongoing representations, which exert influences on visual search. These fragile representations, however, are highly susceptible to visual interferences that share feature dimensions with the memoranda and are presented at the same

locations (Souza & Oberauer, 2016). This explanation could help to interpret our observation in the deterministic retro-cue condition; however, it does not explain the absent attentional capture effects of deprioritized items in the predictive retro-cue and the deterministic pre-cue condition.

Alternatively, a more reasonable explanation suggests that deprioritized items in the deterministic retro-cue condition still receive WM resources due to inefficient resource allocation. This explanation was partially supported when we assessed the attentional capture effect of the deprioritized item for each interval in this condition (Figure 6). When we conducted six one-tailed one-sample t-tests against zero, we found there was a significant attentional capture effect in the first interval (p = 0.01, FDR corrected), but not in the other five intervals. Therefore, the significant larger-than-zero attentional capture effect of the deprioritized item over the entire delay might be driven only by the first interval; that is, irrelevant information was not discarded immediately following the deterministic cue instruction.

Additional evidence comes from a correlation analysis between the effectiveness of memory resource allocation and the final WM outcome. If participants could not effectively allocate memory resources in this deterministic retro-cue condition, their memory performance should be impacted by this ineffectiveness. We quantified the effectiveness of resource distribution with the magnitude difference of attentional capture effects of prioritized and deprioritized items. The correlation result of individual effectiveness, averaged across trials within participants, and memory accuracies revealed a positive relationship between these two measurements (r = 0.47, t(29) = 2.85, p = 0.008), suggesting that participants' memory performances could be modulated by the effectiveness of internal attentional selection.

In contrast, when the cue was presented before encoding, completely task-irrelevant information was not allowed to be encoded into WM. Memory performance in the deterministic

pre-cue condition was actually determined by the extent that irrelevant information was removed from memory maintenance. Dopaminergic processing might be a strong candidate for supporting the filtering mechanisms on incoming information. It has been proposed that the D<sub>1</sub> go pathway allows entry of items into WM, whereas the D<sub>2</sub> no-go corticostriatal pathway prevents it (Frank & O'Reilly, 2006). Thus, the D<sub>2</sub> receptors might be involved in preventing irrelevant information from accessing limited memory resources in the deterministic pre-cue condition (Fallon, Zokaei, Norbury, Manohar, & Husain, 2017).

Ineffective attention allocation was also observed for the predictive retro-cue condition; the deprioritized item was not actively kept during memory maintenance even though it still had a chance to be probed. However, the information that was not actively kept does not mean that it was utterly lost, as the memory accuracy for deprioritized items was still high. As de Silva and Ma (2018) suggested, the memory object with a nonzero probe probability might still receive zero resources when the memory resource is limited. In this predictive cue condition, the process through which participants utilized the cue reliability information might tax WM resources to a greater degree compared to that in the deterministic or nonpredictive cue conditions, therefore leaving fewer resources to be allocated to memory information. In this situation, the deprioritized item might receive zero resource to be kept active. Of course, our result does not exclude the possibility that deprioritized item still receive some resources, but the representation of the deprioritized item might be too imprecise to interact with perception and induce the attentional capture effect (Hollingworth & Hwang, 2013).

Surprisingly, neither the prioritized nor the deprioritized items in the nonpredictive retrocue condition showed traces of internal representations during WM maintenance. Several possibilities could be proposed to explain this phenomenon. First, the memory items might be

stored in a form that did not interact with visual search. As the multiple state account of VWM (Olivers et al., 2011) argued, the number of attentional templates is limited to one at a time, when two or more items of equal relevance are maintained in VWM, multiple representations/attentional templates are expected to compete for access to sensory representations, and this mutual competition may prevent any of the items from making it to the status of attentional template. As a result, the attentional capture effect on the basis of memory representations should be abolished when loading VWM with more than a single item (van Moorselaar, Theeuwes, & Olivers, 2014). van Moorselaar and colleagues (2014) varied memory load from one to four and found that memory-related capture was only restricted to one memory item, regardless of an individual's WM capacity. Moreover, when two equally relevant items were maintained concurrently, they were stored as accessory items and shielded from visual search; however, when one of the two items was prioritized as relevant (the cue was 100% reliable), the prioritized item did interact with visual search, which was in consistent with our result with a deterministic retro-cue.

This sole active VWM representation account seems to provide a good explanation to our nonpredictive retro-cue results; nevertheless, other studies suggested that attention can be controlled by multiple VWM representations (Beck, Hollingworth, & Luck, 2012; Chen & Du, 2017; Irons, Folk, & Remington, 2012). For example, Chen and Du (2017) asked participants to memorize two items with a conjunction of two features and demonstrated that both memory representations could capture attention and interfere with visual search. Previous studies have suggested that neural representations for feature conjunction are enhanced compared to those for a single feature (Woodman & Vogel, 2008). Therefore, perhaps the WM representations in our retro-cue condition, as well as in van Moorselaar et al. (2014)'s study, were not strong enough

when increasing the memory load beyond a single item, whereas WM representations for the feature conjunction were sufficiently active to guide attention.

Lastly, it is also possible that both WM representations were active initially after the offset of retro-cue, but our behavioral method was not temporally sensitive enough to capture this attentional guidance. Previous studies have shown that memory-driven attentional effects decreased with increasing time between the memory colors and the search display, especially when the WM content was easily verbalized (Dombrowe, Olivers, & Donk, 2010). It makes sense that visual representation, not the verbal code, would interfere more with visual attention. In our study, we asked participants to memorize two colors; however, participants could have remembered the color name instead of maintaining a visual representation of the color. Dombrowe et al. (2010) suggested that when the stimulus-onset asynchrony (SOA) was set to 3500 ms (1000 ms memory color duration and 2500 ms interstimulus interval), the influence of the memorized color, which could easily be remembered verbally, on attention was disappeared, while in shorter SOA conditions, the attentional guidance was still present. Our task had 12 consecutive visual search trials, and the overall duration was way beyond 3500 ms. Therefore, the initial visual representation might be converted into a verbal code that no longer affected visual attention.

In the nonpredictive pre-cue condition, the deprioritized and prioritized WM contents exerted influences on visual searches, suggesting that memory representations in the pre-cue condition were stored in a more robust state than in the retro-cue condition. As hypothesized, in this 50% reliable cue condition, the prioritized memory representations were subject to temporal degradation overall, while deprioritized representations changed in a more fluctuated fashion, as revealed by a higher polynomial degree in the polynomial trend analysis.

Many neuroimaging studies also investigated how attended and unattended WM information can be retained. Some recent models postulated that WM contents are retained by changes in synaptic weights rather than persistent stimulus-selective neuronal firing (Mongillo, Barak, & Tsodyks, 2008; Myers, Stokes, & Nobre, 2017; Stokes, 2015), and attended memory items are retained actively while unattended items are retained in an activity-silent form. However, other studies (Christophel, Iamshchinina, Yan, Allefeld, & Haynes, 2018) also pointed out that the absence of stimulus-selective signals for unattended items observed in previous work (LaRocque, Riggall, Emrich, & Postle, 2016; Lewis-Peacock et al., 2012; Wolff et al., 2017) might reflect a lack of sensitivity in the experimental procedures, such as the small number of subjects, the choice of interested brain regions etc. Christophel et al. (2018) used a large pool of 87 subjects and included not only sensory but also parietal and frontal cortex into analysis. Their results suggested that when both memory items are relevant to the task, but one of them is in a more prioritized status, such as in preparation for an upcoming task, there exists different cortical specialization for the prioritized versus deprioritized item. The visual cortex maintains a highresolution representation of the prioritized item, whereas the intraparietal areas and the frontal eye fields maintain low-resolution representations of both the prioritized and deprioritized items. The selective recruitments of the early visual cortex for the retention of prioritized items might be the neural source of their behavioral benefits.

#### **Limitations and Future Directions**

In previous sections, we have discussed that verbalization might be one of the reasons that we failed to observe an attentional capture effect in nonpredictive retro-cue conditions. That does not necessarily mean verbal WM representation does not bias attention during visual search task at all. In fact, previous investigations (Kawashima & Matsumoto, 2017; Soto & Humphreys,

2007) demonstrated that verbal representations in WM can also be used to control visual attentional guidance. However, precluding encoding of items in verbal WM may make the attentional capture effect more detectable. Future studies can prevent verbalization by accompanying the main task with a concurrent articulation task (Downing & Dodds, 2004), or by using a within-category discrimination task (Hollingworth, & Maxcey-Richard, 2013) that requires memory for the precise visual properties of the mnemonic items, or by using visual stimuli from different categories, such as shape or texture, that are harder to verbalize.

Unlike previous studies (Griffin & Nobre, 2003; Gunseli et al., 2015) comparing the neutral cue with probabilistic cues to investigate cueing benefits and costs, our experimental design did not include a neutral cue condition but included a nonpredictive cue condition. Even though the nonpredictive cue condition could not provide any useful information about which memory item would be probed, simply presenting a directional cue might still alter the status of prioritized mental representations; therefore, they might be two distinct cue forms. For example, some studies (Zokaei, Manohar, Husain, & Feredoes, 2014; Zokaei, Ning, Manohar, Feredoes, & Husain, 2014) used an "incidental-cueing" approach, which also employed nonpredictive cues (i.e., 50% reliable when there were two memory targets), and found a performance benefit for prioritized items. Without a neutral cue condition, it is hard for us to compare the cueing advantages for the prioritized representation and disadvantages for the deprioritized representations and disadvantages for the deprioritized representations with other studies. Future studies might want to overcome this shortage and investigate the cueing benefits and costs modulated by different cue types and cue reliabilities.

Our study demonstrated the potential of using the magnitude of attentional capture effect to represent the strength of WM representation. There might exist other proxies representing the WM representations behaviorally. One of these proxies can be eye movement.

Several studies have suggested that there is a close link between working memory and eye movement (Boon, Theeuwes, & Belopolsky, 2019; Theeuwes, Belopolsky, & Olivers, 2009). For example, eye movements might represent an overt (Tremblay, Saint-Aubin, & Jalbert, 2006) and covert (Theeuwes et al., 2009) form of rehearsal during WM maintenance, and the inability to plan eye movement would disrupt performance during the rehearsal stage of spatial WM task (Pearson, Ball, & Smith, 2014). Theeuwes, Olivers, and Chizk (2005) found that when participants were asked to memorize the location of a stimulus, eyes would curve away from the remembered location. Therefore, the saccade curvature could work as a measure to determine whether an item was stored during WM maintenance under different cue reliability conditions.

With a mixed-design study, this dissertation investigated how directing attention in different WM stages and assigning different amounts of memory resources would affect final memory recall, and more importantly, affect how mental representations were stored during a memory delay. Our results replicated many previous findings; however, few studies have manipulated both the cue reliability and cue type, and systematically and extensively investigated their effects on memory retrieval and maintenance. Our results provided some new insights about WM and selective attention. For example, the status of deprioritized memory representations (i.e., kept or lost) is not only depended on the probabilistic cue information but also depended on whether attention is guided externally or internally; probabilistic information overall has a more substantial influence on memory retrieval performance than on the strength of memory representations; the strength of memory representations, at least measured with attentional bias, could be dissociated with final memory performance. Lastly, our study demonstrated the potential of using memory-driven attentional capture to reflect the strength of

maintained WM representations, providing a new direction and behavioral toolbox for probing mental representations, which are typically observed with neuroimaging approaches.

REFERENCES

## REFERENCES

- Astle, D. E., Summerfield, J., Griffin, I., & Nobre, A. C. (2012). Orienting attention to locations in mental representations. *Attention, Perception, & Psychophysics, 74*(1), 146-162.
- Awh, E., Barton, B., & Vogel, E. K. (2007). Visual working memory represents a fixed number of items regardless of complexity. *Psychological science*, *18*(7), 622-628.
- Awh, E., Vogel, E. K., & Oh, S. H. (2006). Interactions between attention and working memory. *Neuroscience*, 139(1), 201-208.
- Backer, K. C., & Alain, C. (2012). Orienting attention to sound object representations attenuates change deafness. *Journal of Experimental Psychology: Human Perception and Performance, 38*(6), 1554.
- Baddeley, A. (1992). Working memory. Science, 255(5044), 556-559.
- Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of memory and language*, 68(3), 255-278.
- Barrouillet, P., & Camos, V. (2012). As time goes by: Temporal constraints in working memory. *Current Directions in Psychological Science*, 21(6), 413-419.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. *R package version*, *1*(7), 1-23.
- Bays, P. M., & Husain, M. (2008). Dynamic shifts of limited working memory resources in human vision. *Science*, 321(5890), 851-854.
- Bays, P. M., Catalao, R. F., & Husain, M. (2009). The precision of visual working memory is set by allocation of a shared resource. *Journal of vision*, 9(10), 7-7.
- Beck, V. M., Hollingworth, A., & Luck, S. J. (2012). Simultaneous control of attention by multiple working memory representations. *Psychological science*, 23(8), 887-898.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal statistical society: series B* (*Methodological*), 57(1), 289-300.
- Boon, P. J., Theeuwes, J., & Belopolsky, A. V. (2019). Updating spatial working memory in a dynamic visual environment. *Cortex*, 119, 267-286.
- Carlisle, N. B., Arita, J. T., Pardo, D., & Woodman, G. F. (2011). Attentional templates in visual working memory. *Journal of Neuroscience*, *31*(25), 9315-9322.

- Chawla, D., Rees, G., & Friston, K. J. (1999). The physiological basis of attentional modulation in extrastriate visual areas. *Nature neuroscience*, *2*(7), 671.
- Chen, Y., & Du, F. (2017). Two visual working memory representations simultaneously control attention. *Scientific reports*, 7(1), 6107.
- Chen, Z., & Cowan, N. (2009). Core verbal working-memory capacity: The limit in words retained without covert articulation. *The Quarterly Journal of Experimental Psychology*, *62*(7), 1420-1429.
- Christophel, T. B., Iamshchinina, P., Yan, C., Allefeld, C., & Haynes, J. D. (2018). Cortical specialization for attended versus unattended working memory. *Nature neuroscience*, 21(4), 494.
- Chun, M. M., Golomb, J. D., & Turk-Browne, N. B. (2011). A taxonomy of external and internal attention. *Annual review of psychology*, *62*, 73-101.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature reviews neuroscience*, *3*(3), 201.
- Cowan, N. (1998). *Attention and memory: An integrated framework* (Vol. 26). Oxford University Press.
- Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and brain sciences*, *24*(1), 87-114.
- Cowan, N., Li, D., Moffitt, A., Becker, T. M., Martin, E. A., Saults, J. S., & Christ, S. E. (2011). A neural region of abstract working memory. *Journal of Cognitive Neuroscience*, 23(10), 2852-2863.
- Cowan, N. (2015). George Miller's magical number of immediate memory in retrospect: Observations on the faltering progression of science. *Psychological review*, *122*(3), 536.
- D'Esposito, M., & Postle, B. R. (2015). The cognitive neuroscience of working memory. *Annual review of psychology, 66,* 115-142.
- de Silva, N., & Ma, W. J. (2018). Optimal allocation of attentional resource to multiple items with unequal relevance. *arXiv preprint arXiv:1802.06456*.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual* review of neuroscience, 18(1), 193-222.
- Dombrowe, I., Olivers, C. N., & Donk, M. (2010). The time course of working memory effects on visual attention. *Visual Cognition*, 18(8), 1089-1112.

- Dowd, E. W., Kiyonaga, A., Beck, J. M., & Egner, T. (2015). Quality and accessibility of visual working memory during cognitive control of attentional guidance: A Bayesian model comparison approach. *Visual Cognition*, 23(3), 337-356.
- Dowd, E. W., Pearson, J. M., & Egner, T. (2017). Decoding working memory content from attentional biases. *Psychonomic bulletin & review*, 24(4), 1252-1260.
- Downing, P. E. (2000). Interactions between visual working memory and selective attention. *Psychological science*, 11(6), 467-473.
- Downing, P., & Dodds, C. (2004). Competition in visual working memory for control of search. *Visual Cognition*, 11(6), 689-703.
- Dube, B., Emrich, S. M., & Al-Aidroos, N. (2017). More than a filter: Feature-based attention regulates the distribution of visual working memory resources. *Journal of Experimental Psychology: Human Perception and Performance, 43*(10), 1843.
- Dube, B., Lumsden, A., & Al-Aidroos, N. (2019). Probabilistic retro-cues do not determine state in visual working memory. *Psychonomic bulletin & review*, *26*(2), 641-646.
- Emrich, S. M., Al-Aidroos, N., Pratt, J., & Ferber, S. (2009). Visual search elicits the electrophysiological marker of visual working memory. *PloS one*, *4*(11), e8042.
- Emrich, S. M., Lockhart, H. A., & Al-Aidroos, N. (2017). Attention mediates the flexible allocation of visual working memory resources. *Journal of Experimental Psychology: Human Perception and Performance*, 43(7), 1454.
- Eriksson, J., Vogel, E. K., Lansner, A., Bergström, F., & Nyberg, L. (2015). Neurocognitive architecture of working memory. *Neuron*, *88*(1), 33-46.
- Ester, E. F., Anderson, D. E., Serences, J. T., & Awh, E. (2013). A neural measure of precision in visual working memory. *Journal of Cognitive Neuroscience*, 25(5), 754-761.
- Ester, E. F., Nouri, A., & Rodriguez, L. (2018). Retrospective cues mitigate information loss in human cortex during working memory storage. *Journal of Neuroscience*, 38(40), 8538-8548.
- Fallon, S. J., Zokaei, N., Norbury, A., Manohar, S. G., & Husain, M. (2017). Dopamine alters the fidelity of working memory representations according to attentional demands. *Journal of cognitive neuroscience*, 29(4), 728-738.
- Fang, M. W., Ravizza, S. M., & Liu, T. (2019). Attention induces surround suppression in visual working memory. *Psychonomic bulletin & review*, 1-8.
- Fazekas, P., & Nanay, B. (2017). Pre-cueing effects: attention or mental imagery?. *Frontiers in Psychology*, *8*, 222.

- Fougnie, D., Suchow, J. W., & Alvarez, G. A. (2012). Variability in the quality of visual working memory. *Nature communications*, *3*, 1229.
- Fox, M. D., Corbetta, M., Snyder, A. Z., Vincent, J. L., & Raichle, M. E. (2006). Spontaneous neuronal activity distinguishes human dorsal and ventral attention systems. *Proceedings* of the National Academy of Sciences, 103(26), 10046-10051.
- Frank, M. J., & O'Reilly, R. C. (2006). A mechanistic account of striatal dopamine function in human cognition: psychopharmacological studies with cabergoline and haloperidol. *Behavioral neuroscience*, 120(3), 497.
- Gazzaley, A., & Nobre, A. C. (2012). Top-down modulation: bridging selective attention and working memory. *Trends in cognitive sciences*, 16(2), 129-135.
- Gazzaley, A., Clapp, W., Kelley, J., McEvoy, K., Knight, R. T., & D'Esposito, M. (2008). Agerelated top-down suppression deficit in the early stages of cortical visual memory processing. *Proceedings of the National Academy of Sciences*, *105*(35), 13122-13126.
- Gazzaley, A., Cooney, J. W., Rissman, J., & D'esposito, M. (2005). Top-down suppression deficit underlies working memory impairment in normal aging. *Nature neuroscience*, 8(10), 1298.
- Giesbrecht, B., Weissman, D. H., Woldorff, M. G., & Mangun, G. R. (2006). Pre-target activity in visual cortex predicts behavioral performance on spatial and feature attention tasks. *Brain research*, *1080*(1), 63-72.
- Gilchrist, A. L., Cowan, N., & Naveh-Benjamin, M. (2008). Working memory capacity for spoken sentences decreases with adult ageing: Recall of fewer but not smaller chunks in older adults. *Memory*, 16(7), 773-787.
- Gilchrist, A. L., Duarte, A., & Verhaeghen, P. (2016). Retrospective cues based on object features improve visual working memory performance in older adults. *Aging, Neuropsychology, and Cognition, 23*(2), 184-195.
- Gorgoraptis, N., Catalao, R. F., Bays, P. M., & Husain, M. (2011). Dynamic updating of working memory resources for visual objects. *Journal of Neuroscience*, *31*(23), 8502-8511.
- Griffin, I. C., & Nobre, A. C. (2003). Orienting attention to locations in internal representations. *Journal of cognitive neuroscience*, 15(8), 1176-1194.
- Gunseli, E., Meeter, M., & Olivers, C. N. (2014). Is a search template an ordinary working memory? Comparing electrophysiological markers of working memory maintenance for visual search and recognition. *Neuropsychologia*, 60, 29-38.

- Gunseli, E., van Moorselaar, D., Meeter, M., & Olivers, C. N. (2015). The reliability of retrocues determines the fate of noncued visual working memory representations. *Psychonomic bulletin & review*, *22*(5), 1334-1341.
- Heuer, A., & Schubö, A. (2016). Feature-based and spatial attentional selection in visual working memory. *Memory & cognition, 44*(4), 621-632.
- Hollingworth, A., & Hwang, S. (2013). The relationship between visual working memory and attention: retention of precise colour information in the absence of effects on perceptual selection. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368*(1628), 20130061.
- Hollingworth, A., & Maxcey-Richard, A. M. (2013). Selective maintenance in visual working memory does not require sustained visual attention. *Journal of Experimental Psychology: Human Perception and Performance*, 39(4), 1047.
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian journal* of statistics, 65-70.
- Hrong-Tai Fai, A., & Cornelius, P. L. (1996). Approximate F-tests of multiple degree of freedom hypotheses in generalized least squares analyses of unbalanced split-plot experiments. *Journal of statistical computation and simulation*, 54(4), 363-378.
- Irons, J. L., Folk, C. L., & Remington, R. W. (2012). All set! Evidence of simultaneous attentional control settings for multiple target colors. *Journal of Experimental Psychology: Human Perception and Performance*, *38*(3), 758.
- Janczyk, M., & Reuss, H. (2016). Only pre-cueing but no retro-cueing effects emerge with masked arrow cues. *Consciousness and cognition*, 42, 93-100.
- Katus, T., Andersen, S. K., & Müller, M. M. (2012). Common mechanisms of spatial attention in memory and perception: a tactile dual-task study. *Cerebral Cortex*, 24(3), 707-718.
- Katus, T., & Eimer, M. (2015). Lateralized delay period activity marks the focus of spatial attention in working memory: evidence from somatosensory event-related brain potentials. *Journal of Neuroscience*, *35*(17), 6689-6695.
- Katus, T., Müller, M. M., & Eimer, M. (2015). Sustained maintenance of somatotopic information in brain regions recruited by tactile working memory. *Journal of Neuroscience*, 35(4), 1390-1395.
- Kawashima, T., & Matsumoto, E. (2017). Cognitive control of attentional guidance by visual and verbal working memory representations. *Japanese Psychological Research*, 59(1), 49-57.

- Kiyonaga, A., & Egner, T. (2013). Working memory as internal attention: Toward an integrative account of internal and external selection processes. *Psychonomic bulletin & review*, 20(2), 228-242.
- Kiyonaga, A., Egner, T., & Soto, D. (2012). Cognitive control over working memory biases of selection. *Psychonomic bulletin & review*, 19(4), 639-646.
- Klyszejko, Z., Rahmati, M., & Curtis, C. E. (2014). Attentional priority determines working memory precision. *Vision research*, 105, 70-76.
- Kuo, B. C., Yeh, Y. Y., Chen, A. J. W., & D'Esposito, M. (2011). Functional connectivity during top-down modulation of visual short-term memory representations. *Neuropsychologia*, 49(6), 1589-1596.
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). ImerTest package: tests in linear mixed effects models. *Journal of Statistical Software*, 82(13).
- Landman, R., Spekreijse, H., & Lamme, V. A. (2003). Large capacity storage of integrated objects before change blindness. *Vision research*, 43(2), 149-164.
- LaRocque, J. J., Lewis-Peacock, J. A., Drysdale, A. T., Oberauer, K., & Postle, B. R. (2013). Decoding attended information in short-term memory: an EEG study. *Journal of cognitive neuroscience*, 25(1), 127-142.
- LaRocque, J. J., Riggall, A. C., Emrich, S. M., & Postle, B. R. (2016). Within-category decoding of information in different attentional states in short-term memory. *Cerebral Cortex*, 27(10), 4881-4890.
- Lepsien, J., Griffin, I. C., Devlin, J. T., & Nobre, A. C. (2005). Directing spatial attention in mental representations: Interactions between attentional orienting and working-memory load. *Neuroimage*, 26(3), 733-743.
- Lepsien, J., & Nobre, A. C. (2006). Attentional modulation of object representations in working memory. *Cerebral cortex*, 17(9), 2072-2083.
- Lewis-Peacock, J. A., Drysdale, A. T., Oberauer, K., & Postle, B. R. (2012). Neural evidence for a distinction between short-term memory and the focus of attention. *Journal of cognitive neuroscience*, 24(1), 61-79.
- Leys, C., Ley, C., Klein, O., Bernard, P., & Licata, L. (2013). Detecting outliers: Do not use standard deviation around the mean, use absolute deviation around the median. *Journal of Experimental Social Psychology*, 49(4), 764-766.
- Li, Q., & Saiki, J. (2015). Different effects of color-based and location-based selection on visual working memory. *Attention, Perception, & Psychophysics,* 77(2), 450-463.

- Linke, A. C., Vicente-Grabovetsky, A., Mitchell, D. J., & Cusack, R. (2011). Encoding strategy accounts for individual differences in change detection measures of VSTM. *Neuropsychologia*, 49(6), 1476-1486.
- Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390*(6657), 279.
- Ma, W. J., Husain, M., & Bays, P. M. (2014). Changing concepts of working memory. *Nature neuroscience*, 17(3), 347.
- Mallett, R., & Lewis-Peacock, J. A. (2018). Behavioral decoding of working memory items inside and outside the focus of attention. *Annals of the New York Academy of Sciences*, 1424(1), 256-267.
- Matsukura, M., Cosman, J. D., Roper, Z. J., Vatterott, D. B., & Vecera, S. P. (2014). Locationspecific effects of attention during visual short-term memory maintenance. *Journal of Experimental Psychology: Human Perception and Performance, 40*(3), 1103.
- Matsukura, M., Luck, S. J., & Vecera, S. P. (2007). Attention effects during visual short-term memory maintenance: protection or prioritization?. *Perception & psychophysics*, 69(8), 1422-1434.
- Mayer, J. S., Bittner, R. A., Nikolić, D., Bledowski, C., Goebel, R., & Linden, D. E. (2007). Common neural substrates for visual working memory and attention. *Neuroimage*, *36*(2), 441-453.
- McElree, B. (1998). Attended and non-attended states in working memory: Accessing categorized structures. *Journal of Memory and Language*, *38*(2), 225-252.
- Miller, G. A. (1956). The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological review*, 63(2), 81.
- Miller, L. M., & D'esposito, M. (2005). Perceptual fusion and stimulus coincidence in the crossmodal integration of speech. *Journal of Neuroscience*, 25(25), 5884-5893.
- Mongillo, G., Barak, O., & Tsodyks, M. (2008). Synaptic theory of working memory. *Science*, *319*(5869), 1543-1546.
- Murray, A. M., Nobre, A. C., Clark, I. A., Cravo, A. M., & Stokes, M. G. (2013). Attention restores discrete items to visual short-term memory. *Psychological science*, *24*(4), 550-556.
- Myers, N. E., Stokes, M. G., & Nobre, A. C. (2017). Prioritizing information during working memory: beyond sustained internal attention. *Trends in Cognitive Sciences*, 21(6), 449-461.

- Myers, N. E., Walther, L., Wallis, G., Stokes, M. G., & Nobre, A. C. (2015). Temporal dynamics of attention during encoding versus maintenance of working memory: complementary views from event-related potentials and alpha-band oscillations. *Journal of cognitive neuroscience*, *27*(3), 492-508.
- Newsome, R. N., Duarte, A., Pun, C., Smith, V. M., Ferber, S., & Barense, M. D. (2015). A retroactive spatial cue improved VSTM capacity in mild cognitive impairment and medial temporal lobe amnesia but not in healthy older adults. *Neuropsychologia*, 77, 148-157.
- Nobre, A. C., Coull, J. T., Maquet, P., Frith, C. D., Vandenberghe, R., & Mesulam, M. M. (2004). Orienting attention to locations in perceptual versus mental representations. *Journal of cognitive neuroscience*, 16(3), 363-373.
- Nouri, A., & Ester, E. F. (2019). Recovery of information from latent memory stores decreases over time. *Cognitive neuroscience*, 1-10.
- Oberauer, K. (2002). Access to information in working memory: exploring the focus of attention. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 28*(3), 411.
- Oberauer, K. (2009). Design for a working memory. In Ross, B. H. (Ed.), *Psychology of learning and motivation: Advances in research and theory* (Vol. 51, pp. 45–100). San Diego, CA: Academic Press.
- Oberauer, K. (2019). Working Memory and Attention–A Conceptual Analysis and Review. *Journal of cognition*, 2(1).
- Oberauer, K., & Lin, H. Y. (2017). An interference model of visual working memory. *Psychological review*, 124(1), 21.
- Olivers, C. N. (2009). What drives memory-driven attentional capture? The effects of memory type, display type, and search type. *Journal of Experimental Psychology: Human Perception and Performance*, *35*(5), 1275.
- Olivers, C. N., & Eimer, M. (2011). On the difference between working memory and attentional set. *Neuropsychologia*, 49(6), 1553-1558.
- Olivers, C. N., Meijer, F., & Theeuwes, J. (2006). Feature-based memory-driven attentional capture: visual working memory content affects visual attention. *Journal of Experimental Psychology: Human Perception and Performance, 32*(5), 1243.
- Olivers, C. N., Peters, J., Houtkamp, R., & Roelfsema, P. R. (2011). Different states in visual working memory: When it guides attention and when it does not. *Trends in cognitive sciences*, *15*(7), 327-334.

- Pearson, D. G., Ball, K., & Smith, D. T. (2014). Oculomotor preparation as a rehearsal mechanism in spatial working memory. *Cognition*, 132(3), 416-428.
- Pertzov, Y., Bays, P. M., Joseph, S., & Husain, M. (2013). Rapid forgetting prevented by retrospective attention cues. *Journal of Experimental Psychology: Human Perception and Performance*, 39(5), 1224.
- Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, 139(1), 23-38.
- Prosser, S. (1995). Aspects of short-term auditory memory as revealed by a recognition task on multi-tone sequences. *Scandinavian audiology*, *24*(4), 247-253.
- Rerko, L., & Oberauer, K. (2013). Focused, unfocused, and defocused information in working memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 39(4), 1075.
- Reynolds, J. H., Pasternak, T., & Desimone, R. (2000). Attention increases sensitivity of V4 neurons. *Neuron*, *26*(3), 703-714.
- Robison, M. K., & Unsworth, N. (2017). Variation in the use of cues to guide visual working memory. *Attention, Perception, & Psychophysics, 79*(6), 1652-1665.
- Schmidt, B. K., Vogel, E. K., Woodman, G. F., & Luck, S. J. (2002). Voluntary and automatic attentional control of visual working memory. *Perception & psychophysics*, 64(5), 754-763.
- Schneider, D., Mertes, C., & Wascher, E. (2015). On the fate of non-cued mental representations in visuo-spatial working memory: Evidence by a retro-cuing paradigm. *Behavioural brain research*, 293, 114-124.
- Serences, J. T., & Yantis, S. (2006). Selective visual attention and perceptual coherence. *Trends in cognitive sciences*, *10*(1), 38-45.
- Shimi, A., Nobre, A. C., Astle, D., & Scerif, G. (2014). Orienting attention within visual short-term memory: Development and mechanisms. *Child development*, 85(2), 578-592.
- Sligte, I. G., Scholte, H. S., & Lamme, V. A. (2008). Are there multiple visual short-term memory stores?. *PLOS one, 3*(2), e1699.
- Singmann, H., Bolker, B., Westfall, J., & Aust, F. (2015). afex: Analysis of factorial experiments. *R package version* 0.13–145.
- Singmann, H., & Kellen, D. (2017). An Introduction to Mixed Models for Experimental Psychology. In D. H. Spieler & E. Schumacher (Eds.), New Methods in Cognitive Psychology. Psychology Press.

- Soto, D., & Humphreys, G. W. (2007). Automatic guidance of visual attention from verbal working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 33(3), 730.
- Soto, D., Humphreys, G. W., & Rotshtein, P. (2007). Dissociating the neural mechanisms of memory-based guidance of visual selection. *Proceedings of the National Academy of Sciences*, 104(43), 17186-17191.
- Soto, D., Heinke, D., Humphreys, G. W., & Blanco, M. J. (2005). Early, involuntary top-down guidance of attention from working memory. *Journal of Experimental Psychology: Human Perception and Performance*, *31*(2), 248.
- Soto, D., Hodsoll, J., Rotshtein, P., & Humphreys, G. W. (2008). Automatic guidance of attention from working memory. *Trends in cognitive sciences*, *12*(9), 342-348.
- Soto, D., Humphreys, G. W., & Heinke, D. (2006). Working memory can guide pop-out search. *Vision research*, *46*(6-7), 1010-1018.
- Souza, A. S. (2016). No age deficits in the ability to use attention to improve visual working memory. *Psychology and Aging*, *31*(5), 456.
- Souza, A. S., & Oberauer, K. (2016). In search of the focus of attention in working memory: 13 years of the retro-cue effect. *Attention, Perception, & Psychophysics, 78*(7), 1839-1860.
- Souza, A. S., Thalmann, M., & Oberauer, K. (2018). The precision of spatial selection into the focus of attention in working memory. *Psychonomic bulletin & review*, 25(6), 2281-2288.
- Sprague, T. C., Ester, E. F., & Serences, J. T. (2016). Restoring latent visual working memory representations in human cortex. *Neuron*, *91*(3), 694-707.
- Sreenivasan, K. K., & Jha, A. P. (2007). Selective attention supports working memory maintenance by modulating perceptual processing of distractors. *Journal of cognitive neuroscience*, 19(1), 32-41.
- Stokes, M. G. (2015). 'Activity-silent'working memory in prefrontal cortex: a dynamic coding framework. *Trends in cognitive sciences*, 19(7), 394-405.
- Theeuwes, J., Belopolsky, A., & Olivers, C. N. (2009). Interactions between working memory, attention and eye movements. *Acta psychologica*, *132*(2), 106-114.
- Theeuwes, J., Olivers, C. N., & Chizk, C. L. (2005). Remembering a location makes the eyes curve away. *Psychological Science*, *16*(3), 196-199.

- Thibault, L., van den Berg, R., Cavanagh, P., & Sergent, C. (2016). Retrospective attention gates discrete conscious access to past sensory stimuli. *PloS one*, *11*(2), e0148504.
- Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature*, 428(6984), 751.
- Tremblay, S., Saint-Aubin, J., & Jalbert, A. (2006). Rehearsal in serial memory for visual-spatial information: Evidence from eye movements. *Psychonomic Bulletin & Review*, 13(3), 452-457.
- van den Berg, R., Shin, H., Chou, W. C., George, R., & Ma, W. J. (2012). Variability in encoding precision accounts for visual short-term memory limitations. *Proceedings of the National Academy of Sciences*, 109(22), 8780-8785.
- van Ede, F., Chekroud, S. R., Stokes, M. G., & Nobre, A. C. (2018). Decoding the influence of anticipatory states on visual perception in the presence of temporal distractors. *Nature communications*, *9*(1), 1449.
- van Moorselaar, D., Olivers, C. N., Theeuwes, J., Lamme, V. A., & Sligte, I. G. (2015). Forgotten but not gone: Retro-cue costs and benefits in a double-cueing paradigm suggest multiple states in visual short-term memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 41*(6), 1755.
- van Moorselaar, D., Theeuwes, J., & Olivers, C. N. (2014). In competition for the attentional template: Can multiple items within visual working memory guide attention?. *Journal of Experimental Psychology: Human Perception and Performance, 40*(4), 1450.
- Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. *Nature*, 438(7067), 500.
- Wallis, G., Stokes, M., Cousijn, H., Woolrich, M., & Nobre, A. C. (2015). Frontoparietal and cingulo-opercular networks play dissociable roles in control of working memory. *Journal* of Cognitive Neuroscience, 27(10), 2019-2034.
- Wildegger, T., Humphreys, G., & Nobre, A. C. (2016). Retrospective attention interacts with stimulus strength to shape working memory performance. *PloS one*, *11*(10), e0164174.
- Wilken, P., & Ma, W. J. (2004). A detection theory account of change detection. *Journal of vision*, *4*(12), 11-11.
- Williams, M., Hong, S. W., Kang, M. S., Carlisle, N. B., & Woodman, G. F. (2013). The benefit of forgetting. *Psychonomic bulletin & review*, *20*(2), 348-355.
- Wolff, M. J., Jochim, J., Akyürek, E. G., & Stokes, M. G. (2017). Dynamic hidden states underlying working-memory-guided behavior. *Nature Neuroscience*, 20(6), 864.

- Woodman, G. F., & Vogel, E. K. (2008). Selective storage and maintenance of an object's features in visual working memory. *Psychonomic bulletin & review*, 15(1), 223-229.
- Ye, C., Hu, Z., Ristaniemi, T., Gendron, M., & Liu, Q. (2016). Retro-dimension-cue benefit in visual working memory. *Scientific reports*, *6*, 35573.
- Yoo, A. H., Klyszejko, Z., Curtis, C. E., & Ma, W. J. (2018). Strategic allocation of working memory resource. *Scientific reports*, 8(1), 16162.
- Zanto, T. P., & Gazzaley, A. (2009). Neural suppression of irrelevant information underlies optimal working memory performance. *Journal of Neuroscience, 29*(10), 3059-3066.
- Zanto, T. P., Rubens, M. T., Thangavel, A., & Gazzaley, A. (2011). Causal role of the prefrontal cortex in top-down modulation of visual processing and working memory. *Nature neuroscience*, 14(5), 656.
- Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature*, 453(7192), 233.
- Zokaei, N., Gorgoraptis, N., Bahrami, B., Bays, P. M., & Husain, M. (2011). Precision of working memory for visual motion sequences and transparent motion surfaces. *Journal of* vision, 11(14), 2-2.
- Zokaei, N., Manohar, S., Husain, M., & Feredoes, E. (2014). Causal evidence for a privileged working memory state in early visual cortex. *Journal of Neuroscience*, *34*(1), 158-162.
- Zokaei, N., Ning, S., Manohar, S., Feredoes, E., & Husain, M. (2014). Flexibility of representational states in working memory. *Frontiers in Human Neuroscience*, *8*, 853.