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Interactions between Attention and Working Memory: Effects of Learning and Task Demands

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Eren Gunseli

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Chapter 1

Introduction

Memory, which “is the process of maintaining information over time” (Matlin, 2005) remains one of the main interests of modern day psychologists, probably because it is so essential for human behavior. Remembering the location of your office, faces of your acquaintances, the meanings of traffic signs, or in some instances your wedding anniversary can be of crucial importance.

Attention, which can be defined as the process of enhancing some information while inhibiting other information, is another crucial aspect of human cognition. As you are reading this, you might also be experiencing people talking and walking around you, some music, a changing landscape through your train window, perhaps even your bodily functions such as heartbeat and respiration. Attention is the process that allows you to focus on the meaning of these sentences by directing your limited cognitive resources to this text and selecting it over all other things happening around you. The focus of this thesis is on the interaction between these two important human cognitive functions; memory and attention.

Mechanisms and types of memory

Memory has been traditionally suggested to be consisting of three types (Atkinson & Shiffrin, 1968). The sensory input from the external world is first maintained in sensory memory for a very brief amount of time. Sensory memory has been suggested to last for fractions of a second but maintain all sensory input. Then, the information flows to short-term memory, or working memory (WM). WM can maintain about 4 items for a duration of seconds (Luck & Vogel, 1997). Information that is continued to be maintained for a longer duration, usually via rehearsal, transfers to long-term memory (Dark & Loftus, 1976; Murdock Jr, 1962). Long-term memory can store a large amount of information for years or even decades.

Although these memory types have been considered as distinct, recent evidence suggests that they might be just different ‘states’ within a single memory type. Specifically, WM has been claimed to represent the relatively more ‘active’, currently relevant, information within long-term memory (Cowan, 2008; McElree, 1998; Oberauer, 2002). Regardless of whether they are different types or states of memory, there is converging evidence to suggest that WM is short-lived, has a low capacity, and is easily accessible, whereas long-term memory is long-lasting, has a high capacity, and is not always easily accessible (Cowan, 2008; Rubin & Wenzel, 1996). This distinction is also supported by case studies that show a double dissociation between WM and long-term memory; including a patient with an impaired WM but an intact long-term memory (Shallice & Warrington, 1970) and vice versa (Scoville & Milner, 1957).

What is a representation?

Through the text I will often talk about representations. A representation is a mental image or construct that represents an idea or object belonging to the external world. A representation can reflect any kind of information such as numbers, pictures or words. Representations are of particular importance when the piece of information they belong to are not present in the external world anymore. For this thesis, the most often visited representations will be memories in the visual domain such as the visual memory representations of your keys, car, or traffic signs.

Interactions between attention and memory

Research has shown that attention and memory are highly interactive (for a review, see Chun & Turk-Browne, 2007). For example attended information is remembered better than unattended information (for reviews, see Awh & Jonides, 2001; Gazzaley & Nobre, 2012). Also, remembered information can guide attention in our visual world. For example, a memory representation of your friend enables you to find him/her in a crowded environment. Both in the internal memories and while attending to external objects, successfully filtering out irrelevant information is essential for daily lives of humans. Humans' ability to successfully select and remember relevant information predicts performance in many cognitive tasks and is correlated with intelligence (Fukuda, Vogel, Mayr, & Awh, 2010; Kane & Engle, 2002; Luck & Vogel, 2013). Therefore, developing a good understanding of attentional selection and memory is important. Since attention and memory are intertwined, a complete understanding of each mechanism depends on studying their interactions. This interaction is crucial for human functioning since there is a constant information flow that needs to be attended and remembered. Consequently, my aim in this dissertation is to contribute to the understanding of visual selective attention, visual working memory (VWM; or short-term memory), long-term memory and their interaction. I will review research, including mine and others, regarding the effects of learning and task demands on 1) guidance of attention *by* memory representations, such as using a memory representation of your keys to find them on a table, and 2) attention *to* memory representations, such as attending to the memory of a billboard picture that you found interesting as opposed to other visual information that you have just experienced while driving like people, cars, and buildings.

Understanding the methodology: EEG

Most of the chapters involve studies that have used electroencheplogram (EEG) recordings on humans. Therefore, I will briefly describe this method. EEG detects electrical activity in the brain using small electrodes attached to the scalp. The electrical activity recorded by the EEG results from ionic current within the neurons of the brain

(Niedermeyer & da Silva, 2005). EEG contains rhythmic activity that is divided into bands of frequencies. A particular band of activity that will be referred to in **Chapter 6** is alpha (8-14 Hz). Alpha band activity recorded over parietal and occipital regions of the scalp has been suggested to reflect, among other behavior depending on the context or task, the active spatial inhibition that is used for attending to relevant information over irrelevant information externally in the world or internally in memory (for a review, see Klimesch, 2012; Van Der Werf, Jensen, Fries, & Medendorp, 2008; van Dijk, van der Werf, Mazaheri, Medendorp, & Jensen, 2010; Worden, Foxe, Wang, & Simpson, 2000).

Another way to study EEG data, which was performed in **Chapters 2, 3** and **4**, is via event-related potentials (ERPs). An ERP is a stereotypic change in neural activity evoked by an 'event', which can be a sensory stimulus or cognitive process, and is typically calculated by averaging EEG data across many instances of this particular event. The averaging boosts the signal-to-noise ratio in the EEG and eliminates the activity that reflects cognitive functions that are *not* time-locked to the particular event of interest. The ERP components that will be analyzed most often in this thesis are the contralateral-delay activity (CDA), the negative two posterior-contralateral (N2pc), and the late positive complex (LPC). The CDA is a widely-studied ERP index of VWM maintenance and has been suggested to index VWM load (Klaver, Talsma, Wijers, Heinze, & Mulder, 1999; McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004). The N2pc has been suggested to reflect the attentional selection of an object over distractors, both in internal representations and the external world (Dell'Acqua, Sessa, Toffanin, Luria, & Jolicœur, 2010; Eimer, 1996; Hickey, Di Lollo, & McDonald, 2009; for a review, see Luck, 2012; Luck & Hillyard, 1994b). Although there are different interpretations of the LPC, the findings point toward a relationship between the LPC amplitude and the effort invested in performing a WM task (Kok, 2001; Polich, 2012; Ruchkin, Johnson, Canoune, & Ritter, 1990).

Finally, recent improvements in data analysis methods have suggested that *patterns* of activity can contain some information that is else not available in the *overall* activity in the EEG (or the BOLD signal of the fMRI for that matter; Norman, Polyn, Detre, & Haxby, 2006). For simplicity, imagine an EEG system with 4 electrodes and two experimental conditions, A and B. Assume that the average electrical activity is equal for A and B, although the patterns of activity across electrodes are different. Using a machine learning approach, a 'classifier' can be trained to discriminate patterns of activity across all electrodes between the two conditions. Then, the classifier can be tested on an independent dataset on its ability to predict which of the two conditions the activity pattern reflects. In **Chapter 6** we have used this approach on time-frequency representations of the EEG data. A successful decoding accuracy at the alpha band for attended locations has been suggested to track the allocation of visual-spatial attention

(Foster, Anderson, Serences, Vogel, & Awh, 2015; Myers, Walther, Wallis, Stokes, & Nobre, 2014; Treder, Bahramisharif, Schmidt, Van Gerven, & Blankertz, 2011).

Part 1. Attention *guided by* Memory: The Role of Memory Representations on the guidance of Visual Attention

Attentional templates in memory

One of the most common paradigms for studying attention acting on the external world is visual search. In the visual search paradigm, a participant aims to find a target object among distractors as fast as possible. Most theories of attention claim that visual search requires a VWM representation that acts as an “attentional template” by specifying the search target (Bundesen, Habekost, & Kyllingsbæk, 2005; Desimone & Duncan, 1995; Wolfe, Cave, & Franzel, 1989). Neurophysiological evidence for these models comes from single-cell recordings in the monkey. Chelazzi, Miller, Duncan, and Desimone (1993) recorded the activity of neurons in the inferior temporal cortex (IT) while the monkey was performing a cued search task. Figure 1 shows the experimental procedure of a cued search task. At this task, the monkey was presented with a search target, and after a blank interval with the search display. Neurons in the IT increased their firing rates when the feature they were selective for appeared as a target cue, and this increase was sustained through the blank interval until the search display. This elevated firing is thought to reflect VWM maintenance of the attentional template. Similar findings have been observed in humans using EEG. The CDA component in the EEG was present during the blank interval between the presentation of the search target and the search display (Carlisle, Arita, Pardo, & Woodman, 2011; Woodman & Arita, 2011). These results indicate that, like in monkeys, an attentional template was maintained in VWM prior to the search.

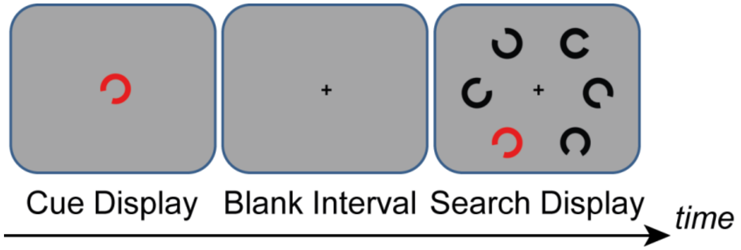

Figure 1.1. Demonstration of a cued search task. The participant is first presented with a cue display that shows the search target. Following a blank interval, the search display is presented. The participant aims finding the target among distractors.

But, in real life, humans often repeatedly search for the same targets instead of being shown a new target each time as in cued search tasks. For example, humans are used to searching for their friends, car keys, or traffic signals, and they know what they are searching without being shown a picture every time. This suggests that the guidance of attention might not be restricted to VWM representations but also involve long-term memory. Evidence for this claim comes from recent human EEG studies. These studies showed that, as participants searched for the same target across trials the amplitude of the CDA decreased suggesting a reduction in the VWM involvement for the maintenance of the attentional template (Carlisle et al., 2011). The search times also decreased across target repetitions, suggesting that participants improved the search task performance. These results show that, while VWM involvement for the maintenance of the attentional template decreases, participants are performing the search faster. This is in line with the theories of learning and automaticity (Anderson, 2000; Logan, 1988; Shiffrin & Schneider, 1977) and suggests that an attentional template transfers from VWM to long-term memory as the same target is repeatedly searched. These findings are in line with previous studies that has shown that long-term memory can guide visual attention (Hutchinson & Turk-Browne, 2012; Olivers, 2011).

However, the aforementioned study that observed a reduction in the CDA used a search task in which maintaining the cue was not necessary for performing the search per se. As seen in Figure 1, the target was a Landolt C with a gap on one side; target repetition consisted of repeating the same gap side on consecutive trials. However, the target in the search display always had a distinct color that was constant through the experimental blocks. Previous studies have shown that visual search is efficient for such color singletons (Duncan & Humphreys, 1989; Theeuwes, 1991, 1992; Treisman & Souther, 1985).[1] As a result, it is likely that participants were using the distinct feature of the target (i.e. the color) for the attentional selection, and were using the gap information only for response selection; that is indicating whether the target matches the cue or not. The efficiency of the attentional selection and its interdependency on the gap direction might make an actively maintained, easily accessible WM template unnecessary, thus facilitate its transfer to LTM. A more demanding visual search on the other hand, as they are typically performed in real life, might require a VWM template even after repeated search for the same target. **Chapter 2** tested this by comparing the rate of decrease in the CDA, as recorded during the retention interval, across blocks of efficient and effortful search tasks. As expected, the search times were lower and the search rate was zero for the efficient search blocks, whereas both the search times and the search rate was higher in

[1] Efficient, or pop-out, search in the literature denotes search in which the search rate, which is the amount of search time per item in the search display, is close to zero. As an example, in an efficient search you would search through 12 items in about the same time as through 6 items. This is the case when the search target has a distinct feature among non-targets, as in Figure 1.

the effortful search blocks. The LPC, which was also recorded during the retention interval, was larger for the effortful search task suggesting that the effort invested for maintaining a template is proportional to the anticipated search difficulty. However, the overall CDA amplitude was equal across search types, suggesting that the CDA is not sensitive to the effort invested maintaining a VWM representation. Finally, the rate of the decrease of the amplitudes of the CDA and the LPC was equal between two search tasks of different difficulty, suggesting that the rapid transfer of the attentional template from VWM to LTM is not exclusive to efficient search but also occurs, at the same speed, for more effortful search situations (**Chapter 2**, Gunseli, Olivers, & Meeter, 2014b).

Is an attentional template a special memory representation?

The studies mentioned above have revealed that both VWM and long-term memory can contribute to visual search by maintaining an attentional template and as a result biasing visual attention to matching objects. This raises the question whether any memory representation can guide attention. Accordingly, we were interested in whether an attentional template is essentially the same as a memory representation used in tasks that do not require attentional guidance, or it is a qualitatively different representation? **Chapter 3** tested this using the CDA, the ERP index of VWM maintenance. We compared the scalp topography, the amplitude, and the decrease in the amplitude of the CDA as a function of repeated task performance across trials, between a visual search task and a simple recognition task. Importantly, only the visual search task but not the simple recognition task involved attentional guidance. Although the responses were slower and less accurate for the search task, all three aforementioned aspects of the CDA were equal across two tasks. On the other hand, the LPC was larger during the blank interval of the search task compared to the simple recognition task. These results suggest that, although greater effort is invested for its maintenance, as indexed by a larger LPC, an attentional template is qualitatively the same as a representation used for simple recognition, at least as can be reflected in the CDA.

One potential limitation of this conclusion is that it is based on the CDA as an index of VWM maintenance. Although the CDA has been repeatedly found to be sensitive to the VWM load, its sensitivity on other features of VWM representations has been controversial. As I have shown in **Chapter 2**, the CDA has been found to be insensitive to the difficulty of the task that the representation is maintained for (also see Ikkai, McCollough, & Vogel, 2010; McCollough et al., 2007). Although some studies observed that the CDA amplitude is larger for maintaining representations that are more complex or precise (Luria, Sessa, Gotler, Jolicœur, & Dell'Acqua, 2010; Luria & Vogel, 2011; Machizawa, Goh, & Driver, 2012; Woodman & Vogel, 2008), other studies have observed that the CDA is not sensitive to the quality of VWM representations (He, Zhang, Li, & Guo, 2015). Therefore, an attentional template might be a special form of VWM, even though this special status does not alter the CDA. If that is the case, then attentional guidance should be exclusive to attentional templates. In other words, if attentional template is a special VWM, then other VWM representations should not be able to guide attention.

Contrary to this claim, behavioral studies using dual memory / search tasks have shown that a VWM representation that is maintained for a *memory task* guides attention during a *search task* even when participants were informed that it can never be the target (Olivers, Meijer, & Theeuwes, 2006; Soto, Heinke, Humphreys, & Blanco, 2005). As seen in Figure 2, in these studies participants performed a visual search task while also maintaining a memory item that was only relevant for a later memory task. I will call this currently irrelevant (but only later relevant) item *accessory*. The search display contained a distractor that on some trials matched the accessory item. Remarkably, the search responses were slower on trials at which the distractor matched the accessory item compared to the trials at which the distractor was not in memory. These results were taken as evidence to claim that VWM representations involuntarily guide attention to matching distractors. This is in line with the claim that a VWM representation that is not maintained for attentional guidance is qualitatively the same as an attentional template. However, some studies that used a variant of this paradigm have failed to observe such involuntary guidance by VWM (Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006; Olivers, 2009; Woodman & Luck, 2007).

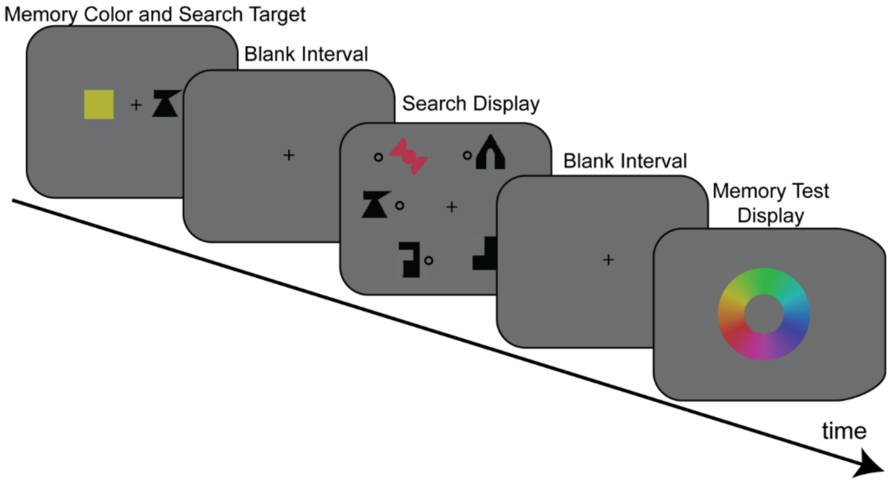

Figure 1.2. An example of a dual memory / search task. Participants are presented with a memory color and a search target. After a blank interval, they perform the search task while maintaining the memory color. After another blank interval, they perform the memory test. In this so-called continuous report memory test, they need to click at the memory color on a circular array of colors. There is a colored distractor in the search display that sometimes matches the color of the memory item. In this example, it is a mismatching color distractor.

Chapter 4 shows that these inconsistent findings can be explained by the memory status of the task-relevant and accessory representations, which are modulated by learning. Previous research has shown that not all VWM representations are equal: The most relevant, or so called prioritized VWM representation is suggested to be maintained in a neurologically more active state than the accessory representations (LaRocque, Lewis-Peacock, & Postle, 2014; Lewis-Peacock, Drysdale, Oberauer, & Postle, 2012; Lewis-Peacock & Postle, 2012; Zokaei, Manohar, Husain, & Feredoes, 2014a). Specifically, attention has been suggested to be guided by the prioritized representation in VWM, but less by accessory representations (Carlisle & Woodman, 2011a; Olivers & Eimer, 2011; for a review, see Olivers, Peters, Houtkamp, & Roelfsema, 2011; Peters, Goebel, & Roelfsema, 2009; Peters, Roelfsema, & Goebel, 2012). Importantly, some studies have suggested that just one item can be prioritized in VWM at a given time (van Moorselaar, Theeuwes, & Olivers, 2014). Moreover, previous research, as mentioned above (also see **Chapter 2** and **Chapter 3**) has shown that a VWM representation is transferred to long-term memory with repeated task performance with the same representation (Carlisle et al., 2011; Gunseli, Meeter, & Olivers, 2014a; Gunseli et al., 2014b; Reinhart, Carlisle, & Woodman, 2014a). We hypothesized that an accessory item is not prioritized, hence does not guide attention, when the search target is new and prioritized in VWM. When the attentional template is transferred to long-term memory as a result of its repeated search, then the accessory item should gain priority within VWM, and hence start involuntarily guiding attention to matching distractors. **Chapter 4** confirmed this hypothesis by showing that a memory matching distractor interfered with search more than a non-memory matching distractor, but only after the same search target was repeated across trials. This result suggests that an accessory representation, although currently task-irrelevant, becomes prioritized and guides attention as the currently relevant representation is transferred to long-term memory. This finding explains why the studies that had a new target defined on every trial failed to find attentional guidance from additional VWM content, whereas those that had a consistent target definition throughout the experiment did find guidance from VWM (Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006; Olivers et al., 2006; Olivers, 2009; Soto et al., 2005).

The results of **Chapter 4** are also important for providing a behavioral support for the claim that repeated search for the same target leads to a transfer of the attentional template from VWM to long-term memory. Although recent ERP studies have shown a reduction in the CDA and the LPC across target repetitions, the course of this reduction was much faster than that in previous studies that have shown learning can take tens or even hundreds of trials (Anderson, 2000; Logan, 1988; Shiffrin & Schneider, 1977). Moreover, these previous behavioral studies have claimed that an improvement in the search *rate* reflects learning and automatization of search. However, the ERP studies observed merely a decrease in response *times,* casting doubt on whether the benefits were due to an improvement in the efficiency with which a target is selected. Hence, one can claim that the small number of target repetitions, unlike the long-runs of repetitions across blocks, do not result in a transfer of a template from VWM to long-term memory, but merely facilitate the efficiency of perceiving the target and/or the response selection. Similarly, it can be hypothesized that that the decrease in the WM-related ERP components might reflect neurological adaptation due to repeated stimulus presentation instead of learning (for a review, see Grill-Spector, Henson, & Martin, 2006). However, we claim that **Chapter 4** argues against these alternative explanations by showing that target repetition leads to the involuntary prioritization of an accessory representation, which is a consequence of the transfer of the target representation to long-term memory. Specifically, we propose that the task-relevant representation must be handed off from VWM in order for a task-irrelevant representation to guide attention, which is in line with previous studies that have shown that a task-irrelevant representation can guide attention only if it is the single representation in VWM (Soto, Greene, Chaudhary, & Rotshtein, 2012; Soto & Humphreys, 2008; van Moorselaar et al., 2014). Thus, **Chapter 4** provides additional support for the claim that a VWM representation rapidly transfers to long-term memory after repeated task performance.

Part 2. Attention *to* Memory: The Role of (Internal) Selective Attention on the Maintenance of VWM Representations

Attentional selection of a memory representation.

In the second part of this dissertation, I focus on the role of attention on the maintenance of representations in VWM. Attentional selection of a memory representation can be described as focusing on a particular representation over the others. There is converging evidence to suggest that attentional focus to a representation will decrease the likelihood of forgetting it. But what happens to unattended representation? Are they forgotten or still remembered? In the literature, there is a controversy regarding fate of unattended representations in memory. Before going into the details, I will briefly describe how attentional selection of memory representations is studied in the laboratory.

Studying the attentional selection of memory representations in the laboratory

There are different ways of facilitating attentional selection of a VWM representation in the laboratory setting. Among the most common ways is using retrospective cues (“retro-cues”). A retro-cue is a cue that indicates which of the several memory representations is likely to be the relevant one for the task at hand. Importantly, a retro-cue is presented after the offset of the memory display, during the blank interval, and therefore acts retrospectively. As seen in Figure 3, most commonly they are visuo-spatial cues pointing the location of the memory item as it was presented on the memory display. Retro-cues have been suggested to result in the attentional selection of the cued representation in a similar way as attentional selection operates on objects in the external world, employing similar brain regions (Nobre et al., 2004). The attentional selection has been claimed to result in better memory performance for the cued representation compared to non-cued representations (Griffin & Nobre, 2003; Lepsien, Griffin, Devlin, & Nobre, 2005; Sligte, Scholte, & Lamme, 2008) as a result of protecting the cued representation from interference by other representations (Pertzov, Bays, Joseph, & Husain, 2013) and new visual input (Makovski, Sussman, & Jiang, 2008; van Moorselaar, Gunseli, Theeuwes, & Olivers, 2015). This protection is established approximately 500 ms following a retro-cue (van Moorselaar et al., 2015).

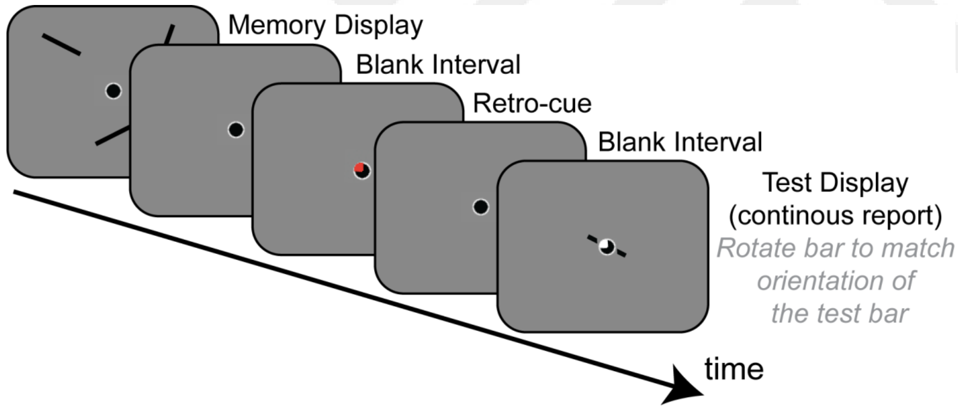

Figure 1.3. An example of a retro-cue in a memory task. Participants are presented with memory display that contains three lines of orientations to be remembered. After a blank interval a retro-cue is presented. A retro-cue is a spatial cue indicating which of the memory items is likely to be tested by retrospectively pointing to its location in the memory display. In this example, it is a red quarter filling on the fixation circle and it points the top-left location. After another blank interval, the test display is presented during which the participant rotates the bar to match the probed memory orientation. In this example, the probed item is the same as the retro-cued item (i.e. the one on the top-left position). Thus, it is a valid retro-cue.

Effects of attending to a VWM representation for attended and unattended information.

Although attending to a representation has been suggested to improve memory performance for the attended representation, the fate of unattended representations is less clear. To study memory for unattended representations, on some proportion of trials a non-cued representation is probed at test. Performance on these *invalid cue* trials is compared to *neutral* or no-cue trials at which none of the representations is cued. An invalid cueing cost means worse memory on invalid trials compared to neutral trials.

Some studies have observed costs of invalid cueing (Matsukura, Luck, & Vecera, 2007; Pertzov et al., 2013) whereas others have not (Landman, Spekreijse, & Lamme, 2003; Rerko & Oberauer, 2013) leading to conflicting conclusions regarding the role of attention on VWM maintenance. An invalid retro-cue cost implies that allocating attention away from VWM representations impairs memory. Accordingly, those that failed to observe an invalid cueing cost have claimed that attention is not necessary for the maintenance of VWM representations, whereas those that observed invalid cueing costs have suggested that attention is necessary for successful VWM maintenance.

Chapter 5 has shown that these inconsistent findings can be due to different retro-cue reliabilities (i.e. the proportion of valid to invalid cue trials) across studies (Gunseli, van Moorselaar, Meeter, & Olivers, 2015). We manipulated the retro-cue reliability across blocks and tested its effects on invalid cueing costs. The invalid cueing costs were absent on blocks in which the retro-cue was 50% valid but present on blocks in which the retro-cue was 80% valid. The valid retro-cue benefit, which is measured by superior performance in valid compared to neutral cue trials, was present for both reliability conditions, though larger for the 80% valid cue blocks. These results are consistent with the previous studies because those that failed to observe invalid cueing costs used lower cue reliabilities (66.6% valid, Landman et al., 2003; 50% valid, Lepsien & Nobre, 2007; 50% valid, Rerko & Oberauer, 2013) compared to the studies that observed invalid cueing costs (80% valid, Astle, Summerfield, Griffin, & Nobre, 2012; 73.5% valid, Matsukura et al., 2007; 70% valid, Pertzov et al., 2013). Based on these results, we suggest that the degree to which participants take retro-cues into account depends on the reliability of the cue. Specifically, participants might be attending more to the cued representation and less to the non-cued representations within VWM when the retro-cue has a higher reliability.

Although these results suggest that the inconsistent results in the literature can be explained by retro-cue reliability, the behavioral data cannot answer whether non-cued representations are forgotten on some proportion of the trials, or whether they are unattended and therefore become more vulnerable to interference from the test display. In order to answer this question we performed a follow-up EEG study. As shown in **Chapter 6**, the N2pc amplitude following the retro-cue was higher when the cue was 80% valid, suggesting that the attentional selection of the cued representation was stronger compared to the 50% valid blocks. Moreover, the accuracy with which the location of the cued representation could be decoded using delay interval alpha band activity was also larger for 80% valid retro-cues, suggesting that the allocation of attention on the cued representation was also stronger through the blank interval. More importantly, the CDA was modulated only following 80% valid cues, suggesting that non-cued representations are forgotten after the retro-cue but only in 80% valid cue blocks. Consistent with

Chapter 5, these results show that the fate of non-cued representations depends on the retro-cue reliability. Non-cued representations can be maintained in memory, or are forgotten depending on the retro-cue reliability that signifies their potential future relevance. Together, these results suggest that attending to a representation does not necessarily entail the loss of non-cued representations (Gunseli et al., 2015; Zokaei, Ning, Manohar, Feredoes, & Husain, 2014b), which suggests that attention and maintenance within VWM are distinct mechanisms, although they are highly interactive.

PART 1

ATTENTION GUIDED BY MEMORY

Chapter 2

Effects of search difficulty on the selection, maintenance, and learning of attentional templates

Gunseli, E., Olivers, C. N., & Meeter, M. (2014). Effects of Search Difficulty on the Selection, Maintenance, and Learning of Attentional Templates. *Journal of Cognitive Neuroscience*.

Abstract

Prominent theories of attention claim that visual search is guided through attentional templates stored in working memory. Recently, the contralateral delay activity (CDA), an electrophysiological index of working memory storage, has been found to rapidly decrease when participants repeatedly search for the same target, suggesting that, with learning, the template moves out of working memory. However, this has only been investigated with pop-out search for distinct targets, for which a strong attentional template may not be necessary. More effortful search tasks might rely more on an active attentional template in working memory, leading to a slower handoff to long term memory, and thus a slower decline of the CDA. Using ERPs, we compared the rate of learning of attentional templates in pop-out and effortful search tasks. In two experiments, the rate of decrease in the CDA was the same for both search tasks. Similar results were found for a second component indexing working memory effort, the late positive complex or LPC. However, the LPC was also sensitive to anticipated search difficulty, as was expressed in a greater amplitude prior to the harder search task. We conclude that the amount of working memory effort invested in maintaining an attentional template, but not the rate of learning, depends on search difficulty.

Introduction

Most models of visual search assume that the brain maintains a working memory representation of the search goal, referred to as the attentional template (Bundesen et al., 2005; Desimone & Duncan, 1995; Duncan & Humphreys, 1989; Wolfe et al., 1989). Neurophysiological and electrophysiological studies using both humans and nonhuman primates have suggested that such attentional templates are indeed maintained in working memory. In these studies, a cue indicated what target to look for in a subsequent search display, which was presented after a blank delay period. During this delay period, single-unit recordings in monkey inferior temporal cortex showed sustained activity to the cue (Chelazzi, Duncan, Miller, & Desimone, 1998; Chelazzi et al., 1993), while in humans, EEG studies have revealed a sustained Contralateral Delay Activity or CDA (Carlisle et al., 2011; Woodman & Arita, 2011), which is regarded as a direct index of visual working memory maintenance (Klaver et al., 1999; McCollough et al., 2007; Vogel & Machizawa, 2004).

Learning an Attentional Template: Role of Long-Term Memory in Guiding Search

A recent ERP experiment by Carlisle et al. (2011, Experiment 3) has suggested that, with target repetition, visual working memory involvement in maintaining the attentional template is reduced. They found that the CDA to the target cue diminished when participants searched for the same target up to 7 times in a row. Putatively, target repetition causes the attentional templates stored in working memory to be transferred to long-term memory.

However, in Carlisle et al. (2011), the cue to which the CDA was measured was not strictly necessary to *find* the target. This was because the target was always defined by a constant, distinct color in the search display. The cue was only necessary to determine whether the target had the correct shape (i.e. it determined the response). Moreover, search is typically very efficient for such color singletons (Duncan & Humphreys, 1989; Theeuwes, 1991, 1992; Treisman & Souther, 1985). Taken together then, the cue in Carlisle et al. (2011) may not necessarily have functioned as an attentional template actively *guiding* search, even though it was required for a correct behavioral *response*. We hypothesized that in more effortful search tasks, in which there is no guidance from a distinct color, search relies to a greater extent on an active attentional template, as maintained in working memory. The greater functional importance of the template in effortful search tasks might lead to a slower handoff to long term memory, and thus a slower decline of the CDA.

This hypothesis was tested in two experiments that compared the rate of learning (as indicated by a decrease in the CDA amplitude across target repetitions) in pop-out and effortful search tasks. Both tasks are illustrated in Figure 1. Participants were shown a target cue, followed, after a delay, by a search display. The distinct target task resembled that used by Carlisle et al. (2011), as the target had a unique color relative to the non-targets. This should aid guidance and make visual search easy and efficient. In contrast, in the non-distinct target task, all stimuli had the same color, so the target did not pop-out from the display, and thus presumably caused search to be more effortful. We ascertained that the two kinds of search indeed differed in efficiency by computing search slopes in each condition.

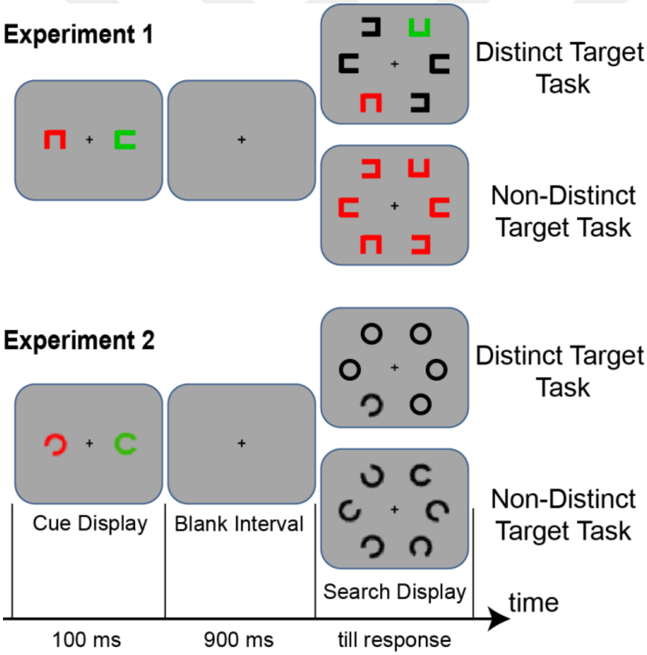

Figure 2.1. Stimulus sequence in both experiments. The search target was defined by color (red in this example). In Experiment 1 (top panel), in the distinct target task the search display contained only one red Landolt square, whereas all items were red in the non-distinct target search display. In Experiment 2 (bottom panel), in distinct target task, the search display had only a single Landolt C, and the distractors were circles. Whereas, all items were Landolt C's in the non-distinct target task. In both tasks the correct response is "present" since all search displays contain the target, i.e. the bottom gap Landolt square in Experiment 1, and bottom-left gap Landolt C in Experiment 2. Note that the sizes and colors are different than the real experiment for illustrative purposes.

Other ERP Components of interest: P170, N2pc, and LPC

In addition to the CDA, we investigated three other ERP components: the P170, N2pc, and the Late Positive Complex or LPC. Recently, Woodman, Carlisle and Reinhart (2013) proposed that the P170 provides a more direct index of the transfer into long-term memory, on the basis of an earlier study linking a reduction in this component to perceptual priming (Voss, Schendan, & Paller, 2010). Consistent with this, Woodman et al. (2013) reported a reduction in P170 amplitude with target repetitions.

Furthermore, if, with target repetition, the attentional template is transferred into long-term memory, then participants might stop attending to the cue, as the memory suffices to do the search. This should lead to a decrease in the N2pc, an index of attentional selection (Eimer, 1996; Hickey et al., 2009; for a review, see Luck, 2012; Luck & Hillyard, 1994b). Contrary to this hypothesis, Carlisle et al. (2011) observed no decline in N2pc across target repetitions, suggesting that participants continued selecting the target cue even after it had been stored in long-term memory.

Because the CDA has been reported to be insensitive to task difficulty (Ikkai et al., 2010; McCollough et al., 2007), we also examined a sustained positive component at central-parietal electrode sites, referred to as the *sustained P3b*, *positive slow wave*, or *late positive complex*, (LPC, Sutton & Ruchkin, 2006). Even though there are different interpretations of the LPC, the findings invariably point towards a relationship between LPC amplitude and the effort required in a working memory task (Kok, 2001; Polich, 2012; Ruchkin et al., 1990). It has been shown that the LPC becomes larger with increasing memory set size (García-Larrea & Cézanne-Bert, 1998; Kusak, Grune, Hagendorf, & Metz, 2000; Ruchkin et al., 1990), and smaller for new items that need to be stored on top of a large existing working memory load (McEvoy, Smith, & Gevins, 1998). In line with this, in dual-task paradigms, the performance on the primary task has been found to be negatively correlated with the LPC amplitude for the secondary task (Isreal, Chesney, Wickens, & Donchin, 1980; Kramer, Wickens, & Donchin, 1985; Paller, McCarthy, & Wood, 1988). Consequently, we used the LPC as an index of the effort invested in maintaining the attentional template. We predicted that more effort would be invested in the template in anticipation of an effortful search task than for a pop-out search task.

Furthermore, using a non-lateralized ERP component as an index of working memory maintenance provided a test for an important alternative explanation of the CDA decline with target repetition. The CDA is a lateralized component; a decline in CDA amplitude could be caused by a decline in working memory maintenance, but also by a decrease in the *laterality* of the working memory representation. Repeated encounter, on varying sides, with the same object might lead to a more ‘centrally’ maintained working memory representation rather than a handoff to a long-term memory representation, and thus to a decrease in laterality. If this would be the case, then the decline in the CDA would be accompanied by a sustained LPC at midline electrodes, showing that working memory effort for maintenance stays intact.

Both the CDA and the LPC are indexes related to working memory maintenance. However, based on the aforementioned literature, we claim that the CDA is a marker for the number of maintained visual-spatial working memory representations, and that the decrease in the CDA reflects handoff of representations from visual working memory to other stores. The LPC, on the other hand, indexes the effort invested in maintaining these working memory representations, and a decrease in the LPC thus reflects less working memory effort. This decrease might either be the result of a handoff from visual working memory, or of devoting less effort for maintaining a representation that is still in working memory – in this case because the search task is anticipated to be easier.

Materials and Methods

Participants

Fourteen and 23 healthy volunteers participated in Experiment 1 and Experiment 2 respectively for course credit or monetary compensation. Seven participants in total were excluded due to excessive noise in their EEG recordings or to ocular artifacts, leaving 12 participants in Experiment 1 (age 20 – 28 years, 9 female) and 18 in Experiment 2 (age 18 – 36 years, 12 female). The study was conducted in accordance with the Declaration of Helsinki, and approved by the faculty's Ethical Committee. Written informed consent was obtained. Due to a technical problem, one participant in Experiment 1 completed 1736 experimental trials rather than 1792, and one participant in Experiment 2 completed 800 experimental trials rather than 840; both were included in the analyses.

Stimuli

Viewing distance was 75 cm. Figure 1 shows an example trial. The background color was gray (58.18 Cd/m^2). The fixation cross, visible throughout the trial, was a black plus sign (0.23° of line length, 0.05° line thickness). In the cue array, a cue and a visually balancing non-cue were presented 1.17° to the left and right of the fixation. In Experiment 1, they were both Landolt squares (0.7° x 0.7°, line thickness 0.1°) with a gap on one side (top, bottom, left or right, 0.68°); one was presented in red (25.70 Cd/m2), the other in green (47.64 Cd/m2). In Experiment 2 they were Landolt C's, i.e. circles (diameter 0.69°, line thickness 0.08°) with a gap of 0.22° on one side of eight possible orientations (top, bottom, left, right, or 45° of rotation off these main directions), again one presented in red and the other in green.

The visual search display contained either six or twelve items, presented equidistantly on an imaginary circle with a radius of 2.9°. In Experiment 1, the items were Landolt squares. In the *distinct target search task,* there was one red and one green item and the rest was black; the target shape could only appear in the cue color. In the *non-*

distinct target search task, items were all the same color as the cue, i.e. either red or green. The search display in Experiment 2 consisted of just one Landolt C among circles in *distinct target search task*, (in target absent trials the single Landolt C had a gap direction that was at least 90° off compared to that of the cue), and in *non-distinct target task*, all items were Landolt C's presented in black.

Design & Procedure

Each trial began with the fixation cross for a randomly jittered duration of 800-1200 ms in Experiment 1, and 1200-1600 ms in Experiment 2. Then, the target cue and the non-target item were presented for 100 ms. For each participant, the target color was constant over the course of the experiments (counterbalanced). In a retention interval of 900 ms, only the fixation cross was presented. The search display was then presented till response. Auditory feedback on accuracy was provided. The inter-trial interval was jittered between 1000 to 1400 ms in Experiment 1, and between 1200 to 1600 ms in Experiment 2. During the inter-trial interval, a word indicated whether the upcoming cue would be the same as the previous trial (OLD) or whether it would be a new one (NEW), following Carlisle et al. (2011). The last 100 ms of the inter-trial interval consisted of only the fixation cross, without the labels OLD or NEW.

The task was to maintain fixation until the search display was presented and then to indicate, as fast as possible without risking accuracy, whether the target was present or absent. In Experiment 1, in case of a target repetition, i.e. when the word "OLD" was presented, participants were asked to verify the target cue in their memory by attending to the cue even though they remembered it from the previous trial in. This instruction was not given in Experiment 2.

Both experiments employed a factorial design with 2 task types (distinct; non-distinct), x 2 set sizes (6; 12), x 2 target presence (present; absent), and an additional factor of target repetitions (1, 3, 6, or 7 trials in Experiment 1, and 2 or 6 trials in Experiment 2). Set size and target presence were randomly mixed within blocks, with equal numbers for each level. The length and number of target repetition runs were chosen to yield a relatively equal distribution of trials per repetition that was still unpredictable for participants; per block, there were four runs of 1, 3, and 7 repetitions and two runs of 6 repetition in Experiment 1. In Experiment 2, there were five runs of both 2 and 6 repetitions per block. In Experiment 1, each participant performed each task type in a separate session (order counterbalanced) on two separate days (0 – 6 days in between, 3.5 days in average).

Before each session, participants completed a practice block of 20 to 24 trials. In Experiment 2, there was a practice block with 6 trials in each task type, 12 trials in total. If accuracy was below 75%, they completed another practice block (1.12 blocks on average, with a maximum of 2 blocks in Experiment 1; in Experiment 2 all participants performed above criterion in the very first target block). In both experiments, before each block, there were also 5 practice trials to familiarize with the particular task type and target color (no particular accuracy requirement this time). The experimental trials consisted of 16 blocks (x 2 sessions) of 56 trials in Experiment 1, and 22 blocks of 40 trials in Experiment 2, with a short break between blocks, during which participants were shown their cumulative average accuracy and response times.

Data Analyses

Degrees of freedom were corrected for sphericity violations using Greenhouse-Geisser epsilon (Jennings & Wood, 1976). Post-ANOVA analyses of multiple comparisons were performed with Student-Newman-Keuls (SNK) tests. Effect of repetition was treated as a linear contrast (Rosenthal & Rosnow, 1985), but the results of the standard omnibus tests were the same (in terms of reaching significance). The RT analyses and all ERP analyses included trials with correct responses only.

Behavioral Analyses

Data were trimmed in two steps. First, trials with a search response faster than 150 ms and slower than 8,000 ms were rejected (< .1 % of all trials for both Experiment 1 and 2), and subsequently those with a search RT of 2.5 standard deviation above or below the mean per condition were excluded. This two-step trimming led to rejection of 2.6% and 2.1% of all trials in Experiment 1 and 2. Further behavioral analyses were performed on target-present trials only. Accuracy and RTs were entered in two repeated measures ANOVAs with the factors task type, set size, and target repetition (results from the Accuracy ANOVAs will not be presented, but were similar to those from the RT ANOVAs).

ERP recording and analysis

The electroencephalogram (EEG) and electro-oculogram (EOG) were recorded from 70 sintered –AG/AgCl electrodes positioned at 64 standard International 10/20 System sites and 6 external locations mentioned below, using the Biosemi ActiveTwo system (Biosemi, Amsterdam, the Netherlands). The ground of ActiveTwo system consists of a feedback loop between the active common mode sense (CMS) electrode and the passive driven right leg (DRL) electrode that "form a feedback loop, which drives the average potential of the subject (the Common Mode voltage) as close as possible to the ADC reference voltage in the AD-box (the ADC reference can be considered as the amplifier "zero")". As a result no impedance measurements or gain adjustments are needed with the ActiveTwo system (www.biosemi.com). The vertical EOG (VEOG) was recorded from electrodes located 2 cm above and below the right eye, and the horizontal EOG (HEOG) was recorded from electrodes 1 cm lateral to the external canthi. The VEOG was used in the detection of blink artifacts, and the HEOG was used in the detection of horizontal eye movement artifacts. Electrophysiological signals were digitized at 512 Hz. ERP analyses were conducted using a combination of Matlab (Mathworks, Natick, MA), the EEGLAB toolbox (Delorme & Makeig, 2004), and ERPLAB toolbox (www.erpinfo.org).

All ERPs were computed with respect to a 200 ms pre-stimulus baseline period and were re-referenced offline to the average of left and right mastoids. The data was filtered with an IIR Butterworth filter with a bandpass of .01 – 40 Hz. Trials with incorrect behavioral responses or with ocular artifacts or large voltage shifts were excluded. Blinks and horizontal eye movements during 200 ms pre-stimulus till 1000 ms post-stimulus interval were identified with a step function that detects whether there is a sudden change in the voltage that exceeds a particular threshold (step-like artifact detection function in ERPLAB toolbox: pop_artstep). The threshold was 60 µV in bipolar VEOG for blinks. The rejection of horizontal eye movements were performed in two steps. First, the single-trial waveforms were inspected to determine an optimum threshold for each participant that rejects a high proportion of the trials with artifacts, while keeping a relatively low proportion of artifact-free trials (Woodman & Luck, 2003). In the second step, the individuals with a residual HEOG activity greater than 3.2 µV (i.e. residual eye movements greater than .2º, propagated voltage greater than .3 µV at posterior sites, see Lins, Picton, Berg, & Scherg, 1993a, 1993b) were excluded from the analyses, which was the ground for exclusion for 2 participants in Experiment 1, and 4 participants in Experiment 2. For participants with more than 10% of trials containing blinks (2 participants in Experiment 1, and one in Experiment 2) an independent component analysis was performed (Makeig, Bell, Jung, & Sejnowski, 1996), and blink artifacts were corrected by removing blink-related independent components. However, the trials at which the blinks occurred during cue presentation were excluded from analyses. In order to detect non-ocular artifacts, a function similar to that applied to EOG channels to detect ocular artifacts was applied to the EEG channels (i.e., the moving window peak-to-peak threshold function in ERPLAB toolbox: pop_ artmwppth), this time with a threshold of 100 µV. Individuals were excluded from analyses if, after all the artifact rejections, the remaining number of trials per bin was lower than 65 trials. This has led to the rejection of 1 additional participant in Experiment 2. For the participants that were involved in the analyses, on average 11.5%, and 11.4% of all trials were rejected by artifact detection functions mentioned above for Experiments 1 and 2 respectively.

The CDA and N2pc were calculated as the difference waves between electrode sites contralateral versus ipsilateral to the location of the target cue. Based on previous studies, the N2pc was measured at P7/8, PO7/8, and O1/2 between 225 to 300 ms (for a review, see Luck, 2012; Sawaki & Luck, 2010) and the CDA at P5/6, P7/8, PO7/8, and O1/2 between 300 to 900 ms after the onset of the cue (McCollough et al., 2007). For the lateralized components, i.e. the N2pc and CDA, we entered the data into an ANOVA with the within-subjects factors of hemisphere (right; left), contralaterality with respect to the target cue (ipsilateral; contralateral), electrode pair (mentioned above), task type (distinct; non-distinct) and target repetition (1; 2&3; 4&5; 6&7 trials in Experiment 1, and 1; 2; 3&4; 5&6 trials in Experiment 2). As the later repetitions occurred progressively less often, for the analyses they were binned into pairs in order to improve signal-to-noise ratio. Only the effects that involve contralaterality will be reported. ANOVAs for non-lateral components, i.e. the P3b, LPC, and P170, had as factors electrode site (Fz; Cz; Pz), task type, and target repetition. Since the time course of the P170, P3b and LPC components are highly dependent on task demands (Kenemans, Kok, & Smulders, 1993; Polich, 2012), we defined them post-hoc on the basis of their observed peak latencies at critical electrodes suggested in the literature; for both experiments, 150-200 ms for the P170, and 475-700 ms for the LPC after the onset of the cue. For the P3b, the intervals were 300-400 ms in Experiment 1 and 330-430 in Experiment 2.

Experiment 1

Results

Behavior

Figure 2 shows the average search RT and search efficiency for each target repetition and task type. Search RT was lower for the distinct target task than for the non-distinct target task, $F(1, 11) = 243.70$, $p < .001$, $\eta_p^2 = .96$, and lower for set size 6 than for set size 12, $F(1, 11) = 124.36$, $p < .001$, $\eta_p^2 = .92$. Response times decreased with increasing target repetition, $F(1, 11) = 11.36$, $p = .006$, $\eta_p^2 = .51$. There was a marginal task type x repetition interaction, $F(1, 11) = 4.27$, $p = .063$, $\eta_p^2 = .28$: As can be seen in Figure 2, repetition was relatively more beneficial in the non-distinct target task. Furthermore, the task type x set size interaction was significant, $F(1, 11) = 140.98$, $p < .001$, $\eta_p^2 = .93$; Set size had a substantial effect in the non-distinct target condition, while it had no effect in the distinct target condition. There was no set size x repetition interaction, $F(1, 11) = .14$, $p = .72$, $\eta_p^2 = .01$, nor was the three-way interaction between set size, repetition, and task type significant, $F(1, 11) = .72$, $p = .42$, $\eta_p^2 = .06$. The accuracy pattern followed that of the RTs except there was no effect of repetition. Accuracy values are shown in Table 1.

Table 2.1. The mean accuracies for both Experiments across set sizes and task types.

Accuracy (%)

	Experiment 1		Experiment 2	
Set Size	6	12	6	12
Distinct Target	94.5	95.2	97.0	96.9
Non-Distinct Target	87.6	81.6	87.7	80.2

Electrophysiology

CDA

Figure 3 shows the CDA waveforms averaged across the electrode pairs used in analyses (P5/6, P7/8, PO7/8 and O1/2). The main effect of contralaterality was significant, $F(1, 11) = 21.13$, $p = .001$, $\eta_p^2 = .66$, indicating that a CDA was triggered by the onset of the cue. This CDA decreased in amplitude with target repetition, as indicated by a significant contralaterality x repetition interaction, $F(1, 11) = 7.77$, $p = .018$, $\eta_p^2 = .41$. SNK tests showed that the CDA for repetition 1 was greater than all the other repetitions, which were not significantly different from each other. The CDA amplitude was equal for both task types, as the task type x contralaterality interaction was not significant, $F(1, 11) = 2.87$, $p = .12$, $\eta_p^2 = .21$. Importantly, the rate of decrease of the CDA for both task types was the same, as suggested by the lack of a task type x contralaterality x repetition interaction, $F(1, 11) = .24$, $p = .64$, $\eta_p^2 = .02$.

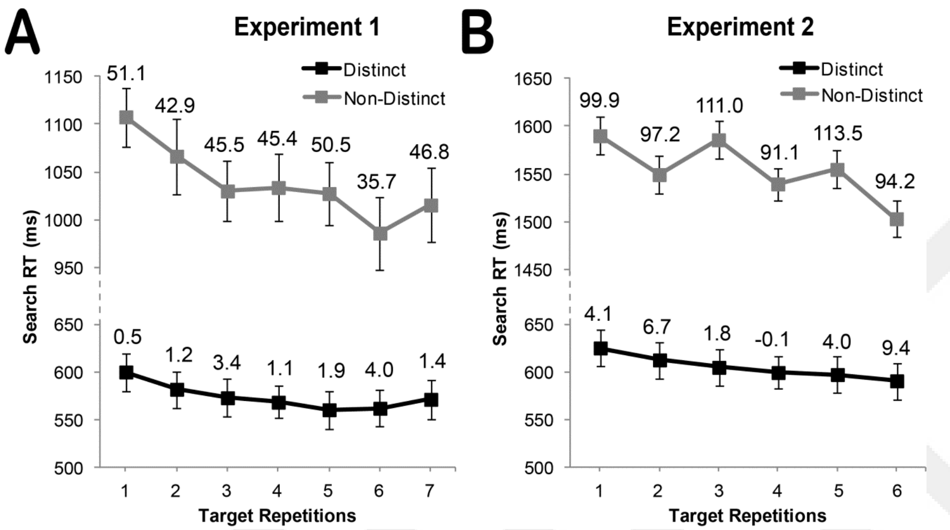

Figure 2.2. Mean search RT and search efficiency (in ms per item, given as the number above each data point) in (a) Experiment 1 and (b) Experiment 2, for the distinct target task (black) and non-distinct target task (gray) trials for each repetition. Target repetitions are given on the x-axis. The error bars represent standard errors of the mean for normalized data, i.e. corrected for between-subjects variance (Cousineau, 2005).

The contralaterality x electrode pair interaction was significant, $F(3, 33) = 4.76$, $p = .007$, $\eta_p^2 = .30$. SNK tests on CDA (contra- minus ipsilateral waves) showed that the CDA amplitude at P7/8 (M = -0.85, SD = 0.79 µV) and PO7/8 (M = -0.79, SD = 0.67 µV) was greater than at O1/2 (M = -0.36, SD = 0.37 µV), while the CDA at P5/6 (M = -0.57, SD = 0.48 µV) was not significantly different from other electrode pairs.

N2pc

Figure 3 also shows N2pc waveforms, which precede those of the CDA. There was a main effect of contralaterality, $F(1, 11) = 41.46$, $p < .001$, $\eta_p^2 = .79$, indicating the presence of a N2pc. The magnitude of the N2pc did not change across target repetitions, as evidenced by the lack of a contralaterality x repetition interaction, $F(1, 11) = 0.20$, $p = .890$, $\eta_p^2 = .01$. There was a task type x contralaterality interaction, $F(1, 11) = 10.71$, $p = .007$, $\eta_p^2 = .49$: The N2pc was larger for the non-distinct target task (M = -1.57, SD = 0.70 µV) than for the distinct target task (M = -1.17, SD = 0.83 µV). There was also a contralaterality x electrode interaction, $F(2, 22) = 13.05$, $p < .001$, $\eta_p^2 = .54$. SNK tests showed that N2pc amplitude was greater at P7/8 (M = -1.71, SD = 0.82 µV) and PO7/8 (M = -1.58, SD = 1.07 µV) than at O1/2 (M = -0.80, SD = 0.61 µV). No other interaction was significant (all Fs < 1.61, ps > .22).

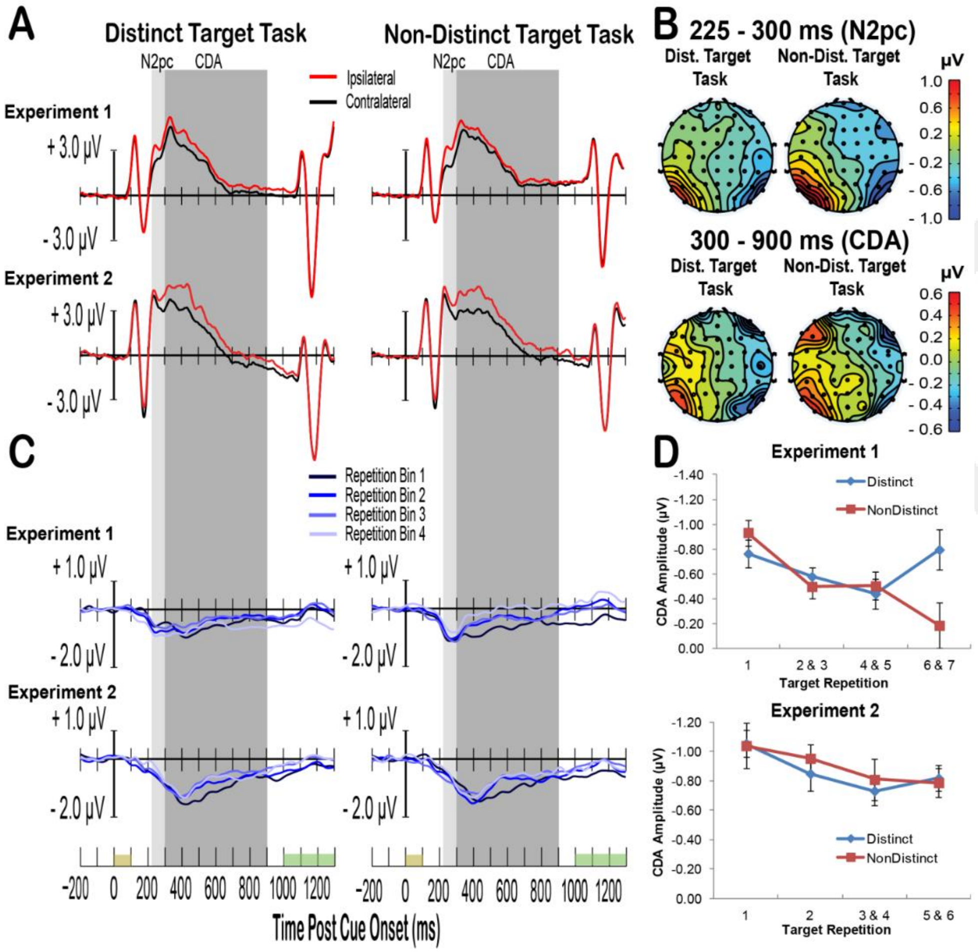

Figure 2.3. (a) The grand average waveforms at the average of PO7/8, P7/8, P5/6, and O1/2 electrode pairs, contralateral (black) and ipsilateral (red) to the location of the cue. Plotted separately are distinct target trials (left panel) and non-distinct target trials (right panel). (b) The scalp distribution of the N2pc and the CDA, in Experiment 1, averaged over their measurement windows, calculated as the voltage distribution in trials in which the cue was presented on the left subtracted from the ones in which it was presented on the right, divided by two. (c) The grand average contralateral minus ipsilateral difference wave, computed from mean amplitude at PO7/8, P7/8, P5/6, and O1/2 electrodes, and low-pass filtered at 5 Hz for visualization purposes, plotted across target repetitions and task types. The shades of blue, from darkest to lightest, stand for repetition 1, repetitions 2&3, 4&5, and 6&7 in Experiment 1 (top panel), and repetition 1, repetition 2, repetitions 3&4, and 5&6 in Experiment 2 (bottom panel). The light gray and dark gray rectangular regions represent the time window at which N2pc and CDA was calculated, respectively. The shadings on the timeline indicates the duration of the cue display (yellow) and the search display (green). Note that positive is plotted upwards. (d) The grand average CDA amplitude in both Experiments as a function of target repetitions. The error bars represent standard errors of the mean for normalized data, i.e. corrected for between-subjects variance (Cousineau, 2005).

P3b and LPC

Figures 4a and 4c show the ERP plots from Fz, Cz, and Pz electrodes, for the P3b and LPC time windows and concomitant scalp topographies. For the P3b, there was a marginal main effect of task type, $F(1, 11) = 3.63$, $p = .083$, $\eta_p^2 = .25$, with a larger P3b in the non-distinct target task. There was no effect of repetition, $F(1, 11) = 1.61$, $p = .231$, $\eta_p^2 = .13$, suggesting that overall P3b amplitude did not decrease with repetitions. There was a main effect of electrode, $F(2, 22) = 10.09$, $p = .006$, $\eta_p^2 = .48$. P3b amplitude at Pz ($M = 4.68$, $SD = 4.26$ µV) was greater than at Cz ($M = 2.40$, $SD = 3.18$ µV) and Fz ($M = 0.79$, $SD = 2.42$ µV). The task type x electrode interaction was significant, $F(2, 22) = 4.52$, $p = .009$, $\eta_p^2 = .41$. Post-hoc SNK tests indicated that the non-distinct target task created a larger P3b than distinct target task at Cz, but not at Fz or Pz. No other interaction reached significance (Fs> 1.86, ps< .199).

For the LPC, there was an effect of target repetition, $F(1, 11) = 11.11$, $p = .007$, $\eta_p^2 = .50$. Like the CDA, the LPC amplitude decreased with target repetition. In contrast to the CDA, the main effect of task type was now also significant, $F(1, 11) = 5.39$, $p = .040$, $\eta_p^2 = .33$; the LPC amplitude was greater in the non-distinct target task than in the distinct target task. There was a main effect of electrode, $F(2, 22) = 64.68$, $p < .001$, $\eta_p^2 = .86$. Positivity at Pz ($M = 3.42$, $SD = 1.23$ µV) was greater than Cz ($M = 1.78$, $SD = 1.35$ µV), and they were both greater than Fz ($M = -.88$, $SD = 1.06$ µV). An electrode x repetition interaction, $F(1, 11) = 4.66$, $p = .054$, $\eta_p^2 = .30$, suggested that the decrease in the LPC amplitude with target repetition was different across electrodes. Post-hoc analyses indicated that the effect of target repetition was present at Pz, and Cz, but not at Fz. As can be seen in Figure 4c, LPC at Pz (the electrode where its amplitude was largest) in the first repetition was greater than the other repetitions, as confirmed by SNK post-hoc tests, replicating the CDA pattern. Neither the electrode x task type interaction, $F(2, 22) = 2.27$, $p = .15$, $\eta_p^2 = .17$, nor the task type x repetition interaction, $F(1, 11) = 2.23$, $p = .16$, $\eta_p^2 = .17$, nor the three-way electrode x task type x repetition interaction, $F(1, 11) = .30$, $p = .59$, $\eta_p^2 = .03$, was significant.

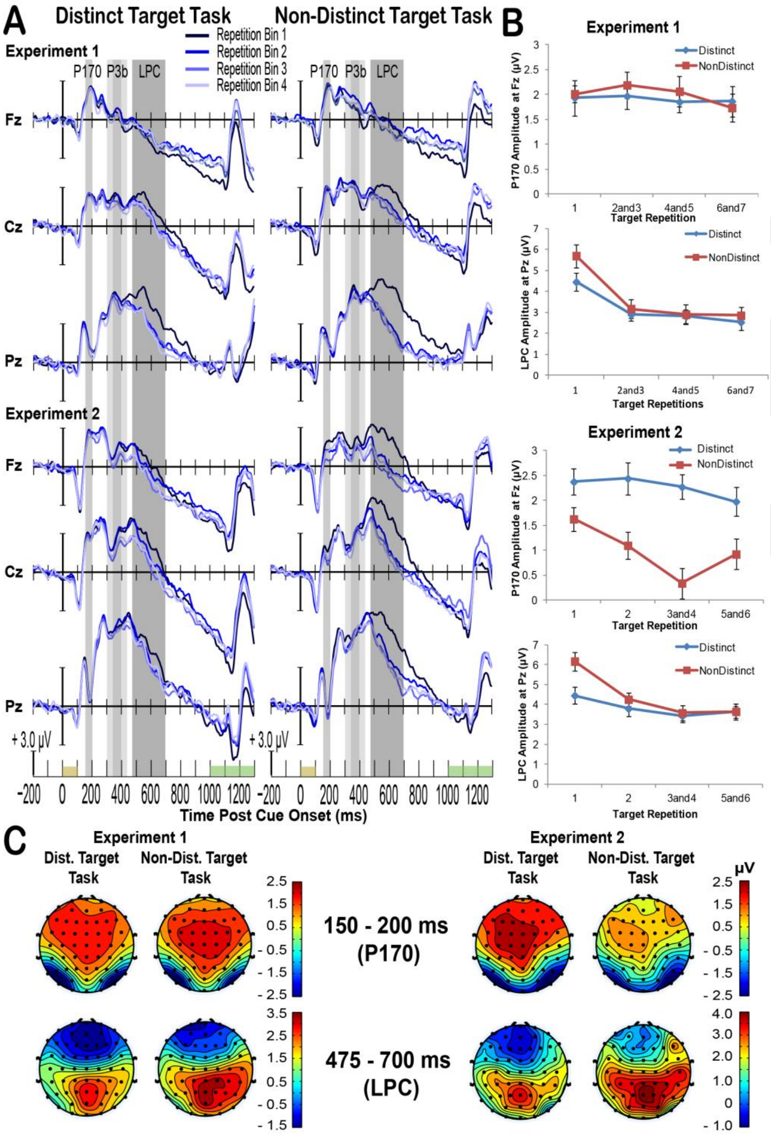

Figure 2.4. (a) The grand average waveforms at the electrodes Fz, Cz, and Pz for distinct target trials (left panel) and non-distinct target trials (right panel). The shades of blue, from darkest to lightest, stand for repetition 1, repetitions 2&3, 4&5, and 6&7 in Experiment 1 (top panel), and repetition 1, repetition 2, repetitions 3&4, and 5&6 in Experiment 2 (bottom panel). The gray rectangular regions represent the time window at which the P170 (150-200ms), P3b (300-400 ms in Experiment 1, and 330-430 ms in Experiment 2), and the LPC (475-700 ms) was calculated The shadings on the timeline indicates the duration of the cue display (yellow) and the search display (green). (b) The grand average P170 amplitude at Fz and grand average LPC amplitude at Pz as a function of repetitions, separately for distinct and non-distinct target trials in Experiment 1 (top panel) and in Experiment 2 (bottom panel). The error bars represent standard errors of the mean for normalized data, i.e. corrected for between-subjects variance (Cousineau, 2005). (c) The scalp topography of P170 (150-200ms, top) and LPC (475-700ms, bottom) seperately for distinct target and non-distinct target trials in Experiment 1 (left panel) and in Experiment 2 (right panel).

P170

Figure 4a also shows the time window at which the P170 was calculated. The P170 magnitude did not differ across target repetition, $F(1, 11) = .80$, $p = .390$, $\eta_p^2 = .07$, nor for task type, $F(1, 11) = .50$, $p = .493$, $\eta_p^2 = .04$. There was a main effect of electrode, $F(2, 22) = 3.96$, $p = .055$, $\eta_p^2 = .27$. SNK tests revealed that the P170 was greater at Fz (M = 1.95, SD = 2.56 µV) and Cz (M = 2.26, SD = 2.79 µV) compared to the Pz (M = 1.65, SD = 2.65 µV). No interaction was significant (Fs < .61, ps > .48).

Discussion

Experiment 1 tested the effects of search difficulty on the processing, maintenance and learning of attentional templates. As expected, search was efficient in the distinct target task (search slope of zero), and not in the non-distinct target task (search slope of ±45 ms per element). ERPs measured to the onset of the cue showed that (1) CDA and LPC amplitudes decreased with target repetition, while the P170, P3b and N2pc did not. For both the CDA and the LPC, the rate of decrease was equal in distinct and non-distinct target search tasks, (2) N2pc, P3b and LPC amplitudes were greater when the anticipated task was more difficult, i.e. in the non-distinct compared to the distinct target search task, but not for the CDA nor the FSP. Contrary to our hypothesis, the former finding indicates that the learning rate of attentional templates is independent of the search difficulty; with target repetition, an attentional template is transferred from working memory to long-term memory at the same rate in efficient and effortful search tasks. At a behavioral level, this transfer was accompanied by a reduction in RT, but not by a reduction in search slope. In other words, search efficiency is not affected by whether an attentional template is maintained in long-term memory or in working memory, at least not for the range of up to seven target instances as measured here.

Anticipated task difficulty affected the mean amplitudes of the LPC and N2pc components. The LPC has been suggested to reflect the effort of working memory processing (García-Larrea & Cézanne-Bert, 1998; Isreal et al., 1980; Kok, 2001; Kramer et al., 1985; Kusak et al., 2000; McEvoy et al., 1998; Paller et al., 1988; Polich, 2012; Ruchkin et al., 1990). Therefore, we suggest that the larger LPC prior to the difficult task shows that maintenance of the attentional template in working memory is performed with a greater effort under difficult search conditions. This effect was not there in the CDA, suggesting that it is not sensitive to task difficulty. Although the CDA and LPC are computed at different electrodes (those at which each is largest), it is not necessarily the case that the difference between CDA and LPC reflects different processing in different brain regions. In fact, when we computed mean amplitude across CDA electrodes (without subtracting contra- and ipsilateral waves, but averaging across all electrodes) , both in the LPC time interval and the original time interval of the CDA, we found a similar sensitivity to task difficulty as in the LPC (see Figure 5a).This suggests that it is the lateral nature of the CDA, not its scalp position, that underlies its differences with the LPC. Since the effect of task difficulty on N2pc was not replicated in the next experiment, we will defer its discussion to Experiment 2.

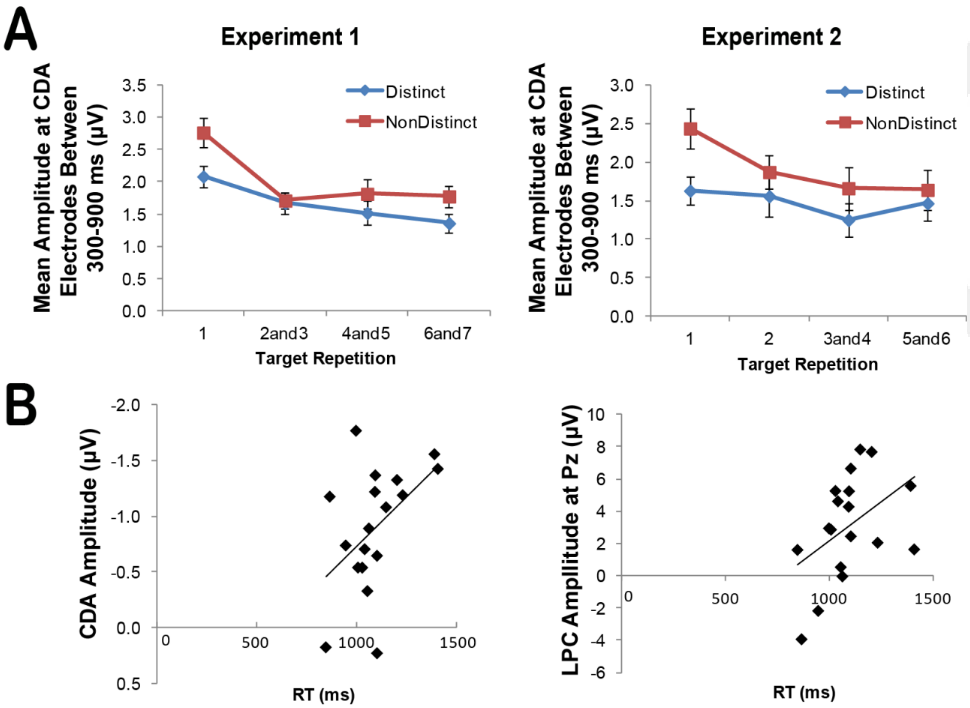

Figure 2.5. (a) Mean amplitude at the electrodes at which the CDA was calculated, i.e. averaging amplitude at electrodes PO7, PO8, P7, P8, P5, P6, O1, and O2,whether or not they are ipsi- and contralateral to the cue, in the interval between 300-900 ms post-cue (the CDA interval), across target repetitions in Experiment 1 (left panel) and in Experiment 2 (right panel). The error bars represent standard errors of the mean for normalized data, i.e. corrected for between-subjects variance (Cousineau, 2005). (b) The relationship between individual participant's behavioral RT and the CDA amplitude (left panel), and the LPC amplitude (right panel) in Experiment 2.

Finally, and contrary to Woodman et al. (2013), here the P170 amplitude did not decline with target repetition. One possibility is that the implicit learning of the various gap directions that the target cue could have was rapidly saturated, leaving little room for the P170 to be affected further by streaks of repetition. Note that we only used four gap directions, and saturation may have been faster than in Woodman et al.(2013) , where eight gap directions were used. In Experiment 2 we therefore used eight gap directions.

Another change we made in Experiment 2 was to take out color in the search displays. Note that in Experiment 1, the easy and difficult search not only differed in difficulty, but also in the use of color to define the target. More specifically, in Experiment 1, the search display in the distinct target task contained one red, one green and several black items whereas it contained only target-colored items in the non-distinct target task. Priming, a form of implicit learning, has been suggested to be dependent on not only the features of the target but also on those of distractors. For example, priming was found to be greater when there is a salient distractor, as in the distinct target task in Experiment 1 of the present study, than when there is none (Meeter & Olivers, 2006). Furthermore, the fact that distractors shared the target color in the non-distinct target task might motivate participants to drop the color value of the cue in that task in order not to be guided to distractors. This manipulation of the cue representation could lead to an extra that underlies the larger LPC in the non-distinct target task. Consequently, any difference in CDA or LPC across task types and target repetitions could be caused by differences in maintaining the color information rather than by search difficulty. [2] To allay these concerns, in Experiment 2 the search displays contained only black stimuli, and all targets were defined by shape (see Figure 1).

Experiment 2

Behavior

Figure 2 shows the average search RT for each target repetition and task type. Search RT was lower for the distinct target task than for the non-distinct target task, $F(1, 17) = 397.68$, $p < .001$, $\eta_p^2 = .96$, and lower for set size 6 than for set size 12, $F(1, 17) = 802.45$, $p < .001$, $\eta_p^2 = .92$. Response times decreased with increasing target repetition, $F(1, 17) = 3.99$, $p = .062$, $\eta_p^2 = .19$. Furthermore, the task type x set size interaction was significant, $F(1, 17) = 582.36$, $p < .001$, $\eta_p^2 = .97$; Set size had a substantial effect in the non-distinct target condition, while it had no effect in the distinct target condition. There was no set size x repetition interaction, $F(1, 17) = .03$, $p = .85$, $\eta_p^2 = .01$, nor was the three-way interaction between set size, repetition, and task type significant, $F(1, 17) = .03$, $p = .86$, $\eta_p^2 = .01$. The accuracy pattern (Table 1) followed that of the RTs except there was no effect of repetition.

[2] We thank Nancy Carlisle for raising this alternative explanation.

Electrophysiology

CDA

Figure 3 shows the CDA waveforms averaged across the electrode pairs used in analyses (P5/6, P7/8, PO7/8 and O1/2). The main effect of contralaterality was significant, $F(1, 17) = 46.59$, $p < .001$, $\eta_p^2 = .73$, indicating that a CDA was triggered by the onset of the cue. This CDA decreased in magnitude with target repetition, as shown by a significant contralaterality x repetition interaction, $F(1, 17) = 6.96$, $p = .017$, $\eta_p^2 = .29$. As in Experiment 1, there was no task type x contralaterality interaction, $F(1, 17) = .09$, $p = .76$, $\eta_p^2 = .01$, and no search task type x contralaterality x repetition interaction, $F(1, 17) = .15$, $p = .904$, $\eta_p^2 = .01$, suggesting that the CDA was the same for the two task types. The contralaterality x electrode pair interaction was significant, $F(3, 51) = 14.34$, $p < .001$, $\eta_p^2 = .46$. SNK tests on CDA (contra- minus ipsilateral waves) showed that the CDA at PO7/8 ($M = -1.18$, $SD = 0.77$ µV) and P7/8 ($M = -1.04$, $SD = 0.49$ µV) was greater than at P5/6 ($M = -0.73$, $SD = 0.65$ µV), and O1/2 ($M = -0.53$, $SD = 0.51$ µV).

N2pc

Figure 3 also shows N2pc waveforms. There was a main effect of contralaterality, $F(1, 17) = 18.22$, $p = .001$, $\eta_p^2 = .52$, indicating the existence of a N2pc. The magnitude of the N2pc did not change across target repetitions, as evidenced by the lack of a contralaterality x repetition interaction, $F(1, 17) = 1.90$, $p = .19$, $\eta_p^2 = .10$. The N2pc was equal in the two tasks, as shown by the lack of task type x contralaterality interaction, $F(1, 17) = .01$, $p = .947$, $\eta_p^2 = .01$. There was a contralaterality x electrode interaction, $F(2, 34) = 7.23$, $p = .002$, $\eta_p^2 = .30$. SNK tests on difference waves showed that N2pc amplitude was greater at P7/8 ($M = -0.73$, $SD = 0.63$ µV) and PO7/8 ($M = -0.81$, $SD = 0.87$ µV) than at O1/2 ($M = -0.42$, $SD = 0.58$ µV). There was a 4-way interaction of task type x repetition x hemisphere x contralaterality, $F(1, 17) = 11.25$, $p = .004$, $\eta_p^2 = .39$, which was not further investigated. No other effect or interaction was significant (all Fs < 1.61, ps > .17).

P3b and LPC

Figures 4a and 4c show the ERP plots from Fz, Cz, and Pz electrodes, for the P3b and LPC time windows and concomitant scalp topography for the LPC. There was a main effect of electrode on P3b, $F(2, 34) = 34.22$, $p < .001$, $\eta_p^2 = .67$. P3b amplitude at Pz ($M = 5.87$, $SD = 2.64$ µV) was greater than at Cz ($M = 2.58$, $SD = 2.46$ µV), and they were both greater than at Fz ($M = 1.11$, $SD = 2.45$ µV). There was no main effect of task type on P3b amplitude, $F(1, 17) = 0.19$, $p = .893$, $\eta_p^2 = .01$, but a main effect of repetition, $F(1, 17) = 4.35$, $p = .052$, $\eta_p^2 = .20$, and an electrode x repetition interaction, $F(1, 17) = 5.49$, $p = .032$, $\eta_p^2 = .24$. Post-hoc analyses showed that the effect of repetition was significant at Fz and Cz, but not at Pz. The task type x electrode interaction was significant, $F(2, 34) = 3.36$, $p = .047$, $\eta_p^2 = .16$, but the SNK tests on the difference values between non-distinct and distinct tasks for P3b did not yield any significant differences for none of the electrodes. No other interaction reached significance (*F*s> .86, *p*s< .67).

For the LPC, there was a main effect of electrode, $F(2, 34) = 32.77$, $p <.001$, $\eta_p^2 = .66$. Positivity at Pz ($M = 4.08$, $SD = 3.32$ µV) was greater than Cz ($M = 1.91$, $SD = 3.32$ µV), and they were both greater than Fz ($M = 0.02$, $SD = 2.27$ µV). There was a main effect of target repetition, $F(1, 17) = 27.89$, $p <.001$, $\eta_p^2 = .62$; the LPC amplitude decreased across repetitions. There was a marginal electrode x repetition interaction, $F(1, 23) = 3.23$, $p =.090$, $\eta_p^2 = .16$, suggesting that the decrease in the LPC amplitude with target repetition was different across electrodes. Post-hoc analyses indicated that the effect of target repetition was nonetheless present at each electrode. Neither the main effect of task type was significant, $F(1, 17) = 3.02$, $p =.100$, $\eta_p^2 = .15$, nor the electrode x task type interaction, $F(2, 34) = 1.44$, $p =.250$, $\eta_p^2 = .08$, suggesting that LPC amplitude, at all electrodes, was equal in the distinct and non-distinct target search tasks. However, there was a significant Task Type x Repetition interaction, $F(1, 17) = 7.75$, $p =.013$, $\eta_p^2 = .31$. As can be seen in Figure 4b, the LPC difference between Distinct and Non-Distinct Target Search Tasks was present at the first repetition but not in further repetitions, as confirmed by SNK tests on the LPC difference between non-distinct and distinct tasks across repetitions. The electrode x task type x repetition interaction was not significant, $F(1, 17) = .76$, $p =.396$, $\eta_p^2 = .04$.

P170

Figure 4a shows waveforms at which the P170 was calculated. There was no effect of electrode, $F(2, 34) = 1.25$, $p = .299$, $\eta_p^2 = .07$. There was a main effect of task type, $F(1, 17) = 17.68$, $p = .001$, $\eta_p^2 = .51$. As seen in Figure 4b, the P170 amplitude was greater in the distinct target task relative to non-distinct target task. There was again no effect of repetition, $F(1, 17) = 1.96$, $p = .180$, $\eta_p^2 = .10$. However, there was a significant electrode x repetition interaction, $F(1, 17) = 4.38$, $p = .052$, $\eta_p^2 = .21$. Post-hoc tests showed that P170 decreased with repetition at Fz, but not at Cz and Pz. Neither the task type x repetition interaction, nor the electrode x task type x repetition interaction was significant, $F(1, 17) = .51$, $p = .485$, $\eta_p^2 = .03$, and $F(1, 17) = .74$, $p = .403$, $\eta_p^2 = .04$, respectively.

Correlations Between Measures of Behavior and ERPs

For both experiments, we investigated whether the ERP measures of working memory correlated with behavioral responses. We partialled out the CDA in LPC-behavioral correlations, and vice versa. In Experiment 2, as seen in Figure 5b, individual mean LPC and mean CDA amplitude were positively correlated with overall RT, with partial correlations of, respectively, $r(15) = .454$, $p=.067$ (bivariate: $r = .415$), and $r(15) = .505$, *p*=.039 (bivariate: *r*= .474); participants with smaller CDAs or LPCs were faster in their responses. These correlations were not significant in Experiment 1, probably due to the smaller set size. Note that both the RT and ERP values were calculated from trials with correct behavioral responses only.

Discussion

The results of Experiment 2 largely replicated those of Experiment 1. Search was fast and more efficient (search slope of zero) in the distinct target task, and slower and effortful (search slope of ±100 ms) in the non-distinct target task. Again, RT decreased with target repetitions but the search efficiency did not. For ERPs, both the CDA and the LPC decreased with target repetitions, the former to an equal extent for both search types. And again, the LPC, but not the CDA, was sensitive to search difficulty, albeit this time only on the first target instance. Moreover, the overall CDA and LPC amplitudes were positively correlated with search RT. This finding is consistent with the theories of learning and automaticity (Logan, 1988), and suggests participants who rely less on the working memory (and presumably more on long-term memory) perform faster on a visual search task (Carlisle et al., 2011).

In contrast to Experiment 1, the P170 now decreased with repetition, suggesting that the number of cue alternatives (here gap directions) indeed plays a role. The main effect of repetition on P170 seems to be mainly driven by non-distinct target condition, although it was not strong enough to yield a significant task type x repetition interaction.

The N2pc results were not consistent with Experiment 1 as this time its amplitude was not sensitive to anticipated search difficulty. Given the lack of a replication of the N2pc sensitivity to search difficulty in Experiment 1 (which we also repeatedly failed to find in other, non-published experiments), we suspect that the N2pc effect in Experiment 1 was a false positive. Alternatively, stimulus complexity might have played a role, as the more complex stimuli of Experiment 2 might have required a strong attentional selection regardless of search difficulty.

General Discussion

In two experiments, we investigated the effects of search task difficulty on selection, maintenance, and learning of the attentional template. Through our set size manipulation, we confirmed that search was efficient (i.e. search slope was zero) in a distinct target condition modeled after Carlisle et al. (2011), while it was much more effortful (resulting in a steeper search slope) in a non-distinct target condition. As predicted, we observed ERP components related to working memory maintenance in the delay period, at electrodes typically reported in the literature: The CDA, maximal at parietal-occipital electrodes (McCollough et al., 2007; Vogel & Machizawa, 2004), and the LPC maximal at central-parietal regions, i.e. Cz and Pz (Polich, 2012; Ruchkin et al., 1990). The most important findings are:

The CDA decreased with target repetition, suggesting that the attentional template was learned after repeated search for the same target (Carlisle et al., 2011). Importantly, search difficulty did not affect the rate of decrease of the CDA. This goes against our hypothesis that more effortful search would require a working memory template in a longer sequence of trials than would efficient search for distinct targets. The rate of learning an attentional template is independent of the search difficulty.

Another index of working memory maintenance, the LPC, also decreased with target repetition, providing additional support for the idea that, with target repetition, the template is learned.

The LPC, but not the CDA, was sensitive to anticipated search difficulty, as its amplitude was greater prior to the non-distinct target task relative to distinct target task. In the light of the literature suggesting that the LPC amplitude reflects the effort invested in working memory processing (García-Larrea & Cézanne-Bert, 1998; Isreal et al., 1980; Kok, 2001; Kramer et al., 1985; Kusak et al., 2000; McEvoy et al., 1998; Paller et al., 1988; Polich, 2012; Ruchkin et al., 1990), this result indicates that anticipating a difficult search results in a greater working memory effort in maintaining an attentional template.

We thus extend the Carlisle et al. (2011) findings by showing that the CDA decreases with target repetition at the same rate when effortful search is required and when participants can rely on efficient search with distinct targets. This finding indicates that the rate of learning an attentional template is independent of the search difficulty. The correlations between both LPC and CDA amplitudes and RT suggests that responses are faster (regardless of accuracy), for participants who perform a handoff of the template to long-term memory faster or to a greater extent.

Furthermore, we show that maintaining an attentional template in working memory is performed with a greater effort when a more difficult search task is anticipated. This effect was mainly evident on the first encounter for a particular cue, as revealed by greater LPC amplitude in the first repetition. Moreover, the LPC findings refute the idea that the decrease in the CDA merely reflects a reduction of lateralization – that is, a shift from lateralized to central memory representations rather than a decrease in maintenance of or effort invested in working memory representations. Since the LPC is measured at midline electrodes, a decrease in lateralization should not affect it. Yet, a decrease in LPC amplitude with repetition was observed, just like for the CDA.

The P3b has been suggested to be sensitive to the level of arousal (Kok, 2001), which may carry over into the LPC. Thus, the sensitivity of the LPC to anticipated task difficulty might be due to greater overall arousal levels. Another marker of arousal is an increased contingent negative variation component or CNV (e.g. Tecce, 1972). Greater arousal would be evident as stronger negativity just before the onset of the search display. Although we did see a negative-going component, possibly a CNV, before the search display, this was not larger for non-distinct target task. Furthermore, considering that the task difficulty was constant thought the blocks rather than being determined by the presentation of the cue, we suggest it is not likely that a general arousal level would to be time-locked to the onset of the cue. Thus, we suggest that the LPC effect in the present study did not reflect differences in the general arousal level, but rather, the amount of effort deployed for maintenance of the attentional template in working memory.

Note that the CDA and the LPC have overlapping scalp distributions and time windows of measurement, but one is a lateralized component while the other is not. Computing non-lateralized activity at CDA electrodes in the CDA time window (and in the LPC time window), we observed a bilateral activity that is sensitive to search difficulty. One explanation would be that the LPC reflects the activity of a general fronto-parietal network involved in attention and working memory functioning (Polich, 2007; Polich, 2012), and since this overall working memory activity may be common to both hemispheres, it could be subtracted out in the computation of a lateral component such as the CDA. This claim is consistent with our interpretation of the two components; the CDA being a marker for the number of maintained visual working memory representations, whereas the LPC being a marker of the amount of effort invested to maintain these representations.

Finally, although the decrease in the CDA and the LPC suggest diminished working memory maintenance and effort respectively, the evidence for a transfer to more implicit memories is rather mixed. Woodman et al. (2013) have recently proposed that a decline in the P170 amplitude provides evidence for transfer to long-term memory, on the basis of a study on priming by Voss et al. (2010). We failed to find such a decline in Experiment 1, but did find it in Experiment 2. One explanation might be in the number of alternative targets (i.e. gap directions). Since the number of target alternatives was larger in Experiment 2 than it was in Experiment 1, a quick saturation of learning may have occurred in Experiment 1, whereas learning in Experiment 2 might have been more gradual, leading to a P170 decline. However, the decrease in CDA and LPC amplitude with repetition would argue against such a lack of learning in Experiment 1. Therefore, we suggest another explanation for the inconsistent P170 results. What has been referred to as the P170 by Voss et al. (2010) and Woodman et al (2013), bears close resemblance to what has been called the FSP (frontal selection positivity), or also anterior P2(a), in previous work on selective attention (Baas, Kenemans, & Mangun, 2002; Kenemans et al., 1993; Potts, 2004; Potts & Tucker, 2001). In those studies, the FSP has been shown to be responsive to the *selection* of task-relevant visual features, rather than their maintenance. If the FSP and P170 are two labels for the same component, then the decrease in P170 amplitude might be an outcome of the feature selection becoming easier, or less relevant, when the target is already stored in long-term memory. Note that with the increase in gap number in Experiment 2, the size of the gaps also became smaller (from 68 º to 22º, the latter being equal to Woodman et al., 2013). This might have made the task-relevant feature initially harder to select than in Experiment 1, but at the same time created more room the FSP/P170 to decline with repetition, as selection became easier. In short, in the light of the literature and results of the present study, we suggest that the decrease of the P170 across target repetition is due to a decline in the frequency or effort of selecting the task relevant feature. Therefore, it is not *indexing* long-term memory consolidation, but rather it is a *consequence* of such a consolidation.

Summary

With repeated targets, participants relied progressively less on a target template stored in working memory, as indicated by a decrease of CDA and LPC amplitudes. Importantly, this shift was independent of whether search was efficient or effortful. However, the anticipation of effortful, as opposed to efficient search did result in increased working memory effort for maintaining the template in working memory, as reflected by a larger LPC. Our results suggest that the functional importance of attentional templates does not affect their rate of long-term memory learning, but only the amount of working memory effort for their maintenance.

Chapter 3

Is a search template an ordinary working memory? Comparing electrophysiological markers of working memory maintenance for visual search and recognition

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Abstract

Visual search requires the maintenance of a search template in visual working memory in order to guide attention towards the target. This raises the question whether a search template is essentially the same as a visual working memory representation used in tasks that do not require attentional guidance, or whether it is a qualitatively different representation. Two experiments tested this by comparing electrophysiological markers of visual working memory maintenance between simple recognition and search tasks. For both experiments, responses were less rapid and less accurate in search task than in simple recognition. Nevertheless, the contralateral delay activity (CDA), an index of quantity and quality of visual working memory representations, was equal across tasks. On the other hand, the late positive complex (LPC), which is sensitive to the effort invested in visual working memory maintenance, was greater for the search task than the recognition task. Additionally, when the same target cue was repeated across trials (Experiment 2), the amplitude of visual working memory markers (both CDA and LPC) decreased, demonstrating learning of the target at an equal rate for both tasks. Our results suggest that a search template is qualitatively the same as a representation used for simple recognition, but greater effort is invested in its maintenance.

Introduction

A large part of everyday life is spent searching for visual objects that are relevant to our current goals, for example when we are looking for a pen to write with, or the ripest fruit in the bowl. Visual search requires a memory representation of the target object, referred to as the search template (or the attentional template, Desimone & Duncan, 1995; Duncan & Humphreys, 1989). Specifically, search templates have been suggested to be maintained in visual working memory (VWM; Desimone & Duncan, 1995). Evidence for this claim comes from electrophysiological and neurophysiological studies on humans and monkeys. In these studies, a cue indicated the target object to search for in a subsequent search display. There was a brief blank interval between the cue and the search displays. During this interval, single-cell recordings in monkeys demonstrated sustained elevated firing in inferior temporal cortex, a high-level visual processing area (Chelazzi et al., 1998; Chelazzi et al., 1993). In humans, electroencephalogram (EEG) recordings have demonstrated the presence of the contralateral delay activity (CDA) during a similar interval (Carlisle et al., 2011; Gunseli, Olivers, & Meeter, in press; Reinhart, Carlisle, & Woodman, 2014b; Woodman & Arita, 2011), which has been suggested to be an index of VWM maintenance (Klaver et al., 1999; McCollough et al., 2007; Vogel & Machizawa, 2004).

There is thus accumulating evidence demonstrating that search templates are maintained in VWM. However, it is unclear whether the neural activity required for maintaining a search template differs than a representation maintained for simple recognition. In visual search, the search template serves to guide attention to the right object in a visual scene containing competing information, and serves to aid in selecting the target over distractors (Rao, Zelinsky, Hayhoe, & Ballard, 2002). These processes are not needed in simple VWM recognition tasks, as participants need typically only to compare the single probe object to the VWM representation of the previously presented cue (especially when memory load is one, Hyun, Woodman, Vogel, Hollingworth, & Luck, 2009; Rensink, 2002). We hypothesized that the additional functions of a search template may entail differences in the neural activity required for its maintenance. To test this hypothesis, we compared visual search to a simple recognition task, and measured event-related potential (ERP) components that provide an electrophysiological index of VWM maintenance of the cue representation.

Figure 1 illustrates the tasks used in the present experiments. Each trial started with the presentation of a cue display, to which the ERPs were measured. After a blank retention interval, the test display was presented. In Experiment 1, we compared a difficult search task, an easier search task, and a simple recognition task. In the search tasks the target had to be found among distractors. This either had to be done on the basis of form, which was inefficient (Gunseli et al., in press), or on the basis of color, which made the search easy and efficient (Duncan & Humphreys, 1989; Theeuwes, 1991, 1992; Treisman & Souther, 1985). In the third, ‘simple recognition’ task, the display contained only a single Landolt C at the center of the screen that had to be compared to the cue. Thus, there was no need for search in this task.

We focused on two ERP components that have been found to reflect neural activity involved in VWM maintenance. The first component, the CDA, is a well-studied component of VWM maintenance. Its amplitude was observed to be greater for bigger memory set sizes (Vogel & Machizawa, 2004), and for maintaining representations that are more complex (Luria et al., 2010; Luria & Vogel, 2011; Woodman & Vogel, 2008) or more precise (Machizawa et al., 2012). These results suggest that the CDA is sensitive to both the quantity and the quality of VWM representations. Moreover, the CDA appears to be sensitive to the amount of attention that is required for the task at hand, as an ongoing multiple object tracking task has been observed to generate a larger CDA than a simple recognition task (Drew, Horowitz, Wolfe, & Vogel, 2011). It can be argued though that this study compared a memory to an attention task, rather than two memory tasks (as was also suggested by different scalp distributions, Dell’Acqua et al., 2010). In the present study we compared different memory tasks: There was always a single object to maintain and the task requirements differed only after the retention interval during which CDA was measured. To our knowledge, no study has investigated whether maintaining the same object, but with a different function in the upcoming task, leads to differences in the quality of a VWM representation, as indexed by the CDA.

The second ERP component of interest was the late positive complex (LPC). This sustained positive component at central-parietal electrode sites has been also referred to as the *positive slow wave.* In some studies it was comprised within a *sustained P3b* (Kok, 2001), but other studies have provided clear evidence for a distinction between a phasic P3b response and a later sustained LPC response (Kok, van de Vijver, & Bouma, 1985; Kusak et al., 2000; Ruchkin & Sutton, 1983; Sutton & Ruchkin, 2006). We too have previously dissociated the P3b and LPC, as we found the latter, but not the former, to be sensitive to the difficulty of the upcoming search task (Gunseli et al., in press). The LPC has been found to be sensitive to memory load (García-Larrea & Cézanne-Bert, 1998; Kusak et al., 2000; Ruchkin et al., 1990), and also to the amount of WM processing (Kok, 2001; Polich, 2012). Consistent with this, it is smaller for maintaining new items in addition to an already high existing WM load (McEvoy et al., 1998). Similarly, in dual-task paradigms, performance on the primary task is negatively correlated with LPC amplitude for the secondary task (Isreal et al., 1980; Kramer et al., 1985; Paller et al., 1988). In the light of these studies, we analyzed the LPC separately from the P3b, and used the LPC as an index of the effort invested in maintaining a VWM representation.

We reasoned that a CDA difference between search and simple recognition tasks would indicate that search templates are stored in a qualitatively different way than VWM representations that are not used for attentional guidance. On the other hand, if the CDA differs also between search tasks, then this effect might be due to differences in task difficulty rather than task type (i.e. search vs. recognition). Moreover, if more effort is invested for maintaining a search template than for a representation used for a simple recognition task, the LPC amplitude should be greater in search tasks. Also, the functional role of search templates could result in the activation of different brain regions for their maintenance relative to other VWM representations (see, Drew et al., 2011). In that case, the scalp distribution of the CDA and/or the LPC could be different across task types. In addition, in Experiment 2, we compared the rate of learning of representations across search and simple recognition tasks. The decrease in CDA and LPC amplitudes across repetitions of the same target in a visual search task has been taken as evidence for learning of search templates, i.e. the handoff of target representations from VWM presumably to long-term memory (Carlisle et al., 2011; Gunseli et al., in press; Reinhart et al., 2014b; Reinhart & Woodman, 2013). This learning has also been observed for VWM representations that are used for a simple recognition task (Reinhart & Woodman, 2013, Experiment 3). In the present study, we compared to learning rate between visual search and recognition tasks in order to investigate whether repeatedly searching for the same target would lead to a different rate of learning than repeatedly maintaining a representation for simple recognition.

Materials and Methods

Participants

Thirty-eight healthy volunteers participated in the experiments for course credit or monetary compensation, 21 in Experiment 1 and 17 in Experiment 2. Six participants in total were excluded; four due to excessive noise in their EEG recordings (see Data Analyses), two to some electrodes having no signal during the recording, leaving 16 participants for each experiment (age 18 – 30 years, 10 female, for Experiment 1; and age 19 – 29 years, 10 female, for Experiment 2) of whom the data was analyzed. The study was conducted in accordance with the Declaration of Helsinki and was approved by the faculty's Ethical Committee. Written informed consent was obtained.

Stimuli

Viewing distance was 75 cm. Figure 1 shows an example trial. The background color was gray (58.18 Cd/m^2). The fixation cross, visible throughout the trial, was a black plus sign (0.23° of line length, 0.05° line thickness). A trial started with a cue array, consisting of a cue and a visually balancing non-cue, presented 1.17° to the left and right of fixation. In

Experiment 1, they were both Landolt squares (0.7° x 0.7°, line thickness 0.1°) with a gap on one side (top, bottom, left or right, 0.68°); one was presented in red (25.70 Cd/m2), the other in green (47.64 Cd/m2). Target cue color was fixed for half a session (see Design & Procedure). In Experiment 2 they were Landolt Cs, i.e. circles (diameter 0.69°, line thickness 0.08°) with a gap of 0.22° on one side of eight possible orientations (top, bottom, left, right, or 45° of rotation off these main directions), again one presented in red and the other in green. Experiment 2 involved a larger stimulus set so that learning could be better studied. Visual search arrays consisted of nine Landolt Squares in Experiment 1, and Landolt Cs in Experiment 2, presented equidistantly on an imaginary circle with a radius of 3.0°. For the sake of simplicity, further in the text, all stimuli will be referred to as Landolt Cs. In Experiment 1, in the *distinct target (easy) search task* there was one red and one green Landolt C and the rest was black, and the target shape could only appear in the target color, while in the *nondistinct target (difficult) search task* Landolt Cs were all in the same color as the cue, i.e. either red or green. In the *simple recognition task* there was only a single Landolt C presented at the center of the screen, which had the same color as the cue. In Experiment 2, the Landolt Cs in the test display were black regardless of the task type.

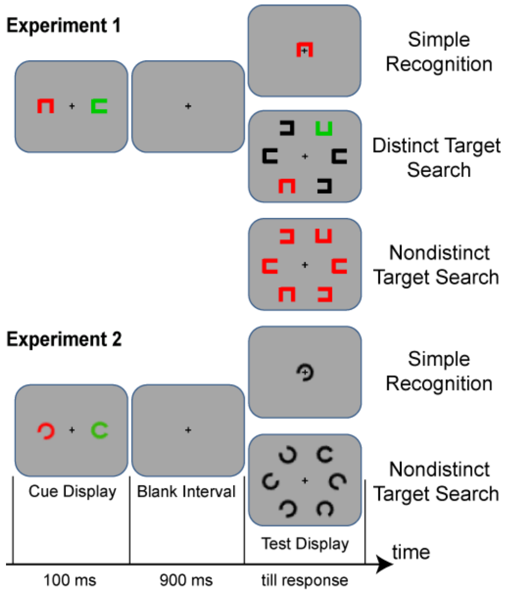

Figure 3.1. Experimental Procedure. The search target was defined by color (red in this example). The cue display contained two Landolt Cs; the target and a hemispherically balancing non-target, that were differentiated by their color. In the test display of the simple recognition task, there was a single Landolt C at the center. In distinct target search task, the test display had a single Landolt C with the target color, leading to an efficient search. In the nondistinct target search task, the colors of the Landolt Cs were all the same leading to an effortful search. In all test displays the correct response is “present” since they contain the target. Note that, for illustrative purposes, the sizes and colors of Landolt Cs, and the set size of the search tasks are different than the real experiments. In the real experiments set size was nine.

Design & Procedure

Each trial began with the fixation cross for a randomly jittered duration of 800-1200 ms in Experiment 1, and 1200-1600 ms in Experiment 2. Next, the target cue and the non-target item were presented for 100 ms. The target color was switched from red to green or vice versa at the half of the experiment (the order counterbalanced across participants). During the retention interval of 900 ms only the fixation cross was presented. Then the test display was presented until response. Auditory feedback on accuracy was provided. The inter-trial interval was jittered between 1200 to 1600 ms. In Experiment 2, during the inter-trial interval a word indicated whether the upcoming cue would be the same as the previous trial (OLD) or whether it would be a new one (NEW), following Carlisle et al. (2011) and Gunseli et al. (in press). The whole inter-trial interval in Experiment 1, and its last 100 ms in Experiment 2, consisted of the fixation cross. The task was to maintain fixation until the test display was presented and then to indicate, as fast as possible without risking accuracy, whether the target was present or absent. Participants were informed that, at the test display of the distinct target search task, only the Landolt C with the target color could have the target gap.

Experiment 1 employed a factorial design with 3 task types (simple recognition; distinct target search; nondistinct target search), x 2 target presence (present; absent), Experiment 2 with 2 task types (simple recognition; nondistinct target search), x 3 target repetitions (1, 4, or 5 trials), x 2 target presence (present; absent). Target presence varied equally and randomly across trials for each block. In Experiment 1, the gap direction of the cue was randomly selected in each trial. In Experiment 2, where the gap directions were sometimes repeated across trials, the length and number of target repetition runs were chosen to yield a relatively equal distribution of trials per repetition that was still unpredictable for participants.

At the beginning of each experiment, there was an initial practice block of 5 trials per task type (15 trials in Experiment 1 and 10 trials in Experiment 2). If accuracy was below 75%, participants completed another practice block (Experiment 1: 1.22 blocks on average, with a maximum of 2 blocks; Experiment 2: 1.35 blocks on average, with a maximum of 3 blocks). Furthermore, before each block, there were 5 practice trials to get used to the particular task type and target color (no particular accuracy requirement this time). There were 12 blocks of 56 experimental trials in Experiment 1, and 20 blocks of 44 experimental trials in Experiment 2, with a short break between blocks in which participants were shown their cumulative average accuracy and response times.

Data Analyses

Degrees of freedom were corrected for sphericity violations using Greenhouse-Geisser epsilon (Jennings & Wood, 1976). Post-ANOVA analyses of multiple comparisons were performed with Student-Newman-Keuls (SNK) tests. Effect of repetition was treated as a linear contrast (Rosenthal & Rosnow, 1985). The RT analyses and all ERP analyses included trials with correct behavioral responses only.

Behavioral Analyses

Data were trimmed in two steps. First, trials with a search response faster than 150 ms and slower than 8,000 ms were rejected (< .1 % of all trials for both Experiment 1 and 2), and subsequently those with a search RT of 2.5 standard deviation above or below the mean per condition were excluded. This two-step trimming led to rejection of 2.6% and 2.3% of all trials in Experiment 1 and 2. Further behavioral analyses were performed on target-present trials only. Accuracy and RTs were entered in two repeated measures ANOVAs with the factors task type (for both experiments) and target repetition (for Experiment 2 only).

ERP recording and analysis

The electroencephalogram (EEG) and electro-oculogram (EOG) were recorded from 70 sintered –AG/AgCl electrodes positioned at 64 standard International 10/20 System sites and 6 external locations mentioned below, using the Biosemi ActiveTwo system (Biosemi, Amsterdam, the Netherlands). No impedance measurements or gain adjustments are needed with the ActiveTwo system (www.biosemi.com). The vertical EOG (VEOG) was recorded from electrodes located 2 cm above and below the right eye, and the horizontal EOG (HEOG) was recorded from electrodes 1 cm lateral to the external canthi. The VEOG was used in the detection of blink artifacts, and the HEOG was used in the detection of horizontal eye movement artifacts. Electrophysiological signals were digitized at 512 Hz. ERP analyses were conducted using a combination of Matlab (Mathworks, Natick, MA), the EEGLAB toolbox (Delorme & Makeig, 2004), and ERPLAB toolbox (Lopez-Calderon & Luck, 2014)

All ERPs were computed with respect to a 200 ms pre-stimulus baseline period and were re-referenced offline to the average of left and right mastoids. The data was filtered with an IIR Butterworth filter with a bandpass of .01 – 40 Hz. Trials with incorrect behavioral responses or with ocular artifacts or large voltage shifts were excluded. The artifact detection was performed on the standard methods of our lab (see Gunseli et al., in press), using the artifact detection functions of the ERPLAB toolbox. The rejection of horizontal eye movements was performed in two steps. First, the single-trial waveforms were inspected to determine an optimum threshold for each participant that rejected a high proportion of the trials with artifacts, while keeping a relatively low proportion of artifact-free trials (Woodman & Luck, 2003). In the second step, the individuals with a residual HEOG activity greater than 3.2 µV (i.e. residual eye movements greater than .2º, propagated voltage greater than .3 µV at posterior sites, see Lins et al., 1993a, 1993b) were excluded from the analyses, which was the ground for exclusion for 2 participants in Experiment 1. Individuals were excluded from analyses if, after all the artifact rejections, the remaining number of trials per bin was lower than 80 trials. This led to the rejection of 1 additional participant in Experiment 1, and the 1 and only rejected participant in Experiment 2. For the participants that were involved in the analyses, on average 13.6%, and 12.7% of all trials were rejected by artifact detection functions mentioned above for Experiments 1 and 2 respectively.

The CDA was calculated as the difference waves between electrode sites contralateral versus ipsilateral to the location of the target cue. Based on previous studies, the CDA was measured at P5/6, P7/8, PO7/8, and O1/2 between 300 to 900 ms after the onset of the cue (McCollough et al., 2007). We entered the CDA data into an ANOVA with the within-subjects factors of hemisphere (right; left), contralaterality with respect to the target cue (ipsilateral; contralateral), electrode pair (mentioned above), task type (simple recognition; distinct target search - for Experiment 2 only; nondistinct target search) and for Experiment 2, target repetition (1; 2&3; 4&5 trials). As the later repetitions occurred progressively less often, for the analyses they were binned into pairs in order to improve signal-to-noise ratio. Only the effects that involve contralaterality were reported. The LPC was calculated between 475-700 ms after the onset of the cue (see Gunseli et al., in press) and was entered into an ANOVA with the within-subjects factors of electrode site (Fz; Cz; Pz), task type, and target repetition. We have also analyzed the P3b, as the peak around 300 ms following the onset of the cue (Gunseli et al., in press; Kusak et al., 2000; Ruchkin & Sutton, 1983; Sutton & Ruchkin, 2006), averaged between 330-430 ms in Experiment 1, and 275-375 ms in Experiment 2, based on the timing of observed average waveform peaks.

Since the interpretation of the null effect of task type on the CDA was critical to our conclusion that a search template is not different from a VWM representation used for simple recognition task, as a post-hoc approach, we calculated Bayes Factors for repeated measures ANOVA, in order to quantify the likelihood of the null hypothesis over the alternative hypothesis, in which r was set a priori to 1.0 (Rouder, Speckman, Sun, Morey, & Iverson, 2009).

Experiment 1. Maintenance of VWM representations across search and recognition tasks

Results

Behavior

Figure 2 shows the average search RT and error rate for each task type. The main effect of task type on RT was significant, $F(2, 30) = 223.33$, $p < .001$, $\eta_p^2 = .94$. Follow-up SNK tests indicated that RT was lowest in the simple recognition task, higher in the distinct target search task, and highest in the nondistinct target search task. The error rate pattern was similar to that of the RT. The main effect of task type on error rate was significant, $F(2, 30) = 47.85$, $p < .001$, $\eta_p^2 = .76$. Follow-up SNK tests showed that participants were more accurate on simple recognition trials and distinct target search trials than on nondistinct target search trials, whereas the former two were no different from each other.

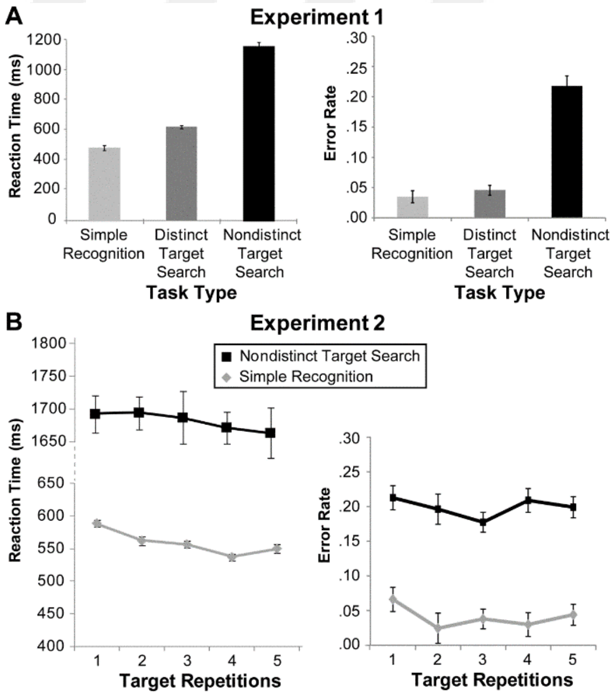

Figure 3.2. Behavioral Results. Mean reaction time (RT, left panel) and error rate (right panel) in the nondistinct target search task (black), distinct target search task (dark gray), and simple recognition task (light gray) trials for (a) Experiment 1 and (b) Experiment 2, where for the latter, target repetitions are given on the x-axis. The error bars represent standard errors of the mean for normalized data, i.e. corrected for between-subjects variance (Cousineau, 2005).

Electrophysiology

Figure 3 shows the CDA waveforms averaged across the electrode pairs used in analyses (P5/6, P7/8, PO7/8 and O1/2). There was a main effect of contralaterality, $F(1, 15) = 17.35$, $p = .001$, $\eta_p^2 = .54$, indicating that a CDA was triggered by the onset of the cue. There was no evidence that the CDA amplitude was different across task types, as the task type x contralaterality interaction was not significant, $F(2, 30) = .74$, $p = .481$, $\eta_p^2 = .05$. There was a contralaterality x electrode pair interaction, $F(3, 45) = 5.43$, $p = .008$, $\eta_p^2 = .27$; follow-up SNK tests on the CDA (contra- minus ipsilateral waves) showed that the CDA amplitude at P7/8 (M = -0.89, SD = 0.63 µV) was greater than the CDA at P5/6 (M = -0.56, SD = 0 (Machizawa et al., 2012).68 µV) and at O1/2 (M = -0.51, SD = 0.56 µV), and the CDA at PO7/8 (M = -0.84, SD = 0.97 µV) was greater than the CDA at O1/2. No other interaction involving contralaterality was significant (all Fs < 2.75, ps > .105). Consistent with the ANOVA, the Bayes Factor analysis indicated that the null hypothesis (no difference in CDA between task types) was 9.9 times more likely to be true than the alternative hypothesis (a CDA difference between task types), JZS Bayes Factor (null\alternative) = 9.9 (Rouder et al., 2009).

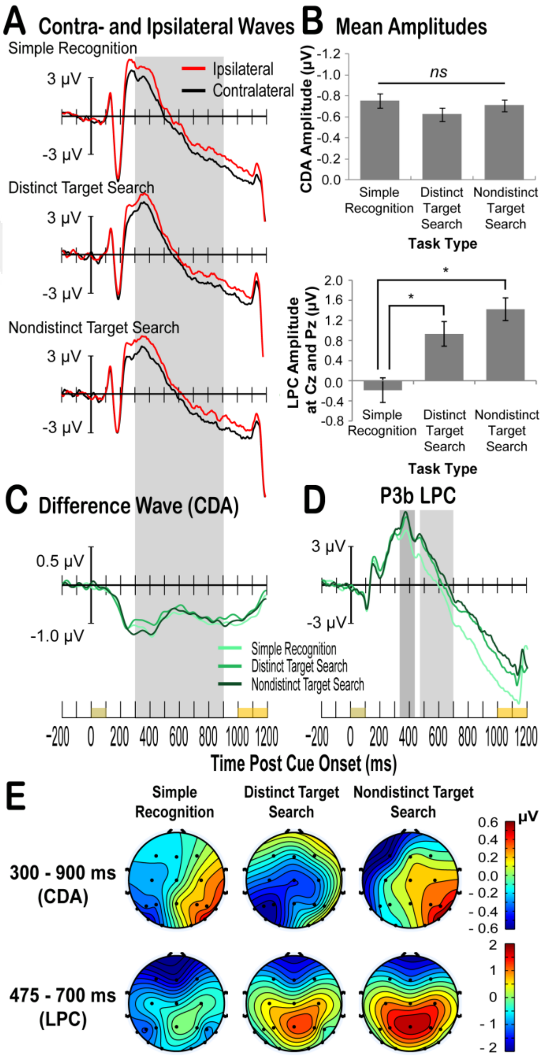

Figure 3.3. ERP results from Experiment 1. (a) The grand average waveforms at the average of PO7/8, P7/8, P5/6, and O1/2 electrodes, contralateral (black) and ipsilateral (red) to the location of the cue, plotted separately for each task type. The shadings on the timeline indicate the duration of the cue display (dark yellow) and the search display (light yellow). Note that positive is plotted upwards. (b) Plots of grand average CDA and LPC amplitudes given separately for each task type. The error bars represent standard errors of the mean for normalized data, i.e. corrected for between-subjects variance (Cousineau, 2005). (c) The grand average waveform of CDA across task types that are shown in shades of green. The CDA was computed as contralateral minus ipsilateral difference wave, between 300-900 ms (marked with the gray rectangular region), from mean amplitude at PO7/8, P7/8, P5/6, and O1/2 electrodes, and low-pass filtered at 5 Hz for visualization purposes. (d) The grand average waveform of P3b (300-400 ms) and LPC (475-700 ms), averaged across Cz and Pz, the electrodes where the LPC amplitude was largest, given separately across target repetitions shown in shades of blue. (d) The scalp distribution of the CDA (top panel), averaged over 300-900 ms, calculated as the voltage distribution in trials in which the cue was presented on the right subtracted from the ones in which it was presented on the left, and divided by two. And the scalp distribution of the LPC (bottom panel) calculated as the mean voltage distribution across 475-700 ms.

Figure 3 also shows the grand average LPC waveforms calculated at Cz and Pz, the electrodes where its amplitude was largest (see below). Overall, the main effect of task type was significant, $F(2, 30) = 5.72$, $p = .008$, $\eta_p^2 = .28$. Follow-up SNK tests indicated that, as seen in Figure 3b, the LPC amplitude in both nondistinct target search task and distinct target search task was greater than in simple recognition task. There was a main effect of electrode, $F(2, 30) = 11.69$, $p = .001$, $\eta_p^2 = .44$. SNK tests yielded that the LPC at Pz ($M = 1.17$, $SD = 2.56$ µV) and at Cz ($M = 0.27$, $SD = 2.43$ µV) were not different than each other and both were greater than at Fz ($M = -1.20$, $SD = 2.00$ µV). There was an electrode x task type interaction, $F(4, 60) = 2.64$, $p = .069$, $\eta_p^2 = .15$. Separate repeated measures ANOVA tests at each electrode demonstrated that the effect of task type was present at Pz, $F(2, 30) = 10.39$, $p < .001$, $\eta_p^2 = .41$, and Cz, $F(2, 30) = 4.54$, $p = .024$, $\eta_p^2 = .12$, but not at Fz, $F(2, 30) = 1.90$, $p = .168$, $\eta_p^2 = .11$ (see Figure 3d).

There was a main effect of electrode on P3b amplitude, $F(2, 30) = 28.70$, $p < .001$, $\eta_p^2 = .65$. There was no significant effect of task type, $F(2, 30) = 2.17$, $p = .132$, $\eta_p^2 = .13$. SNK tests yielded that the P3b was greatest at Pz ($M = 5.35$, $SD = 3.81$ µV), smaller at Cz ($M = 3.17$, $SD = 3.04$ µV), and smallest at Fz ($M = 1.42$, $SD = 1.77$ µV). The electrode x task type interaction was significant, $F(4, 60) = 6.00$, $p = .003$, $\eta_p^2 = .29$. Separate ANOVAs at each electrode showed that the effect of task type was significant only at Pz, $F(2, 30) = 4.79$, $p = .022$, $\eta_p^2 = .24$, but not at Fz or Cz (Fs<1.72, ps>.19).

The relationship between an individual's ERP amplitudes and behavioral performance was investigated computing Spearman's rank-order correlations, which is less sensitive to outliers than Pearson's product-moment correlations, since one participant had an RT more than 2.5 SD above the group average. As seen in Figure 4a, for the simple recognition task, the mean LPC amplitude calculated at Cz and Pz, the electrodes where its amplitude was largest, correlated with mean RT, $r_s(16) = .574$, $p = .020$. The other correlations were not significant (ps>.202).

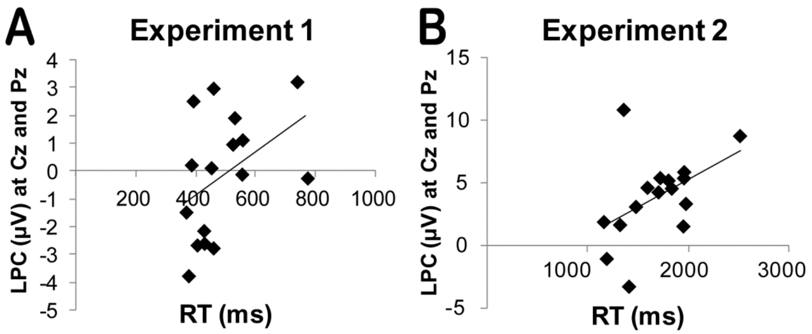

Figure 3.4. ERP – Behavior Correlations. The relationship between individual participant's RT and the LPC amplitude (a) in Experiment 1 for the simple recognition task, and (d) in Experiment 2 for the nondistinct target search task.

Discussion

Experiment 1 tested the effects of task type on the maintenance of VWM representations. More specifically, it compared, between a simple recognition task and two search tasks (of different difficulty), the amplitudes and scalp distributions of the CDA and the LPC components for maintaining a VWM representation. The simple recognition task, which did not involve a visual search, was performed more rapidly than both visual search tasks, and the distinct target search task was performed more rapidly and accurately than the nondistinct target search task. These results suggest that, as expected, performance was easiest at the simple recognition task and hardest at the nondistinct search task.

In terms of ERPs, the LPC was greater in both search tasks compared to the simple recognition task. This effect was strongest at the electrodes at which the LPC itself was strongest (Pz and Cz), suggesting that the distribution of the LPC over electrodes did not change, only its amplitude. These results indicate that anticipating a search task, compared to a simple recognition task, leads to greater working memory effort invested in maintaining the task-relevant-VWM-representation. Recently, Gunseli et al. (in press) observed a greater LPC for maintaining a search template when the upcoming search task was more difficult, although in this Experiment 1, the LPCs were statistically indistinguishable between search tasks. Consequently, we propose that the amount of effort invested for maintenance depends on the relative differences in the difficulty that a participant experiences across tasks, rather than reflecting a function-specific difference between search and recognition. Furthermore, for the simple recognition task, participants with smaller LPCs were faster suggesting that individuals who invest less effort in WM maintenance are able to perform the relevant task faster (Gunseli et al., in press). The P3b followed a similar pattern to LPC as its amplitude was sensitive to task type, although this effect was significant only at Pz.

Neither the scalp distribution of the CDA nor its amplitude was sensitive to the task type. These results are also in line with Gunseli et al. (in press), who observed equal CDAs for maintaining a VWM representation for search tasks of different difficulty, and extends it further by demonstrating that the CDA amplitude is also independent of whether the representation is used for search or simple recognition. Therefore, we conclude that, in terms of these ERP markers, search templates are qualitatively the same as VWM representations used for recognition, although greater effort is invested for their maintenance. In Experiment 2, we investigated whether differences in the upcoming function (e.g. search vs. no-search) of a representation would affect its rate of learning when it is repeatedly presented across trials.

Experiment 2. Learning of VWM representations across search and recognition tasks

Previous research has shown that repeated search for the same target leads to learning – that is, a handoff from VWM to presumably long-term memory, as evidenced by a decrease in CDA amplitude (Carlisle et al., 2011; Gunseli et al., in press). A similar learning has been observed for representations that are used in a simple recognition task (Reinhart & Woodman, 2013). Experiment 2 tested whether the rate of learning is different between these two tasks that require the representation for different functions. To decrease the likelihood of saturation of learning across trials, in Experiment 2, we increased the cue set size by using Landolt C's with eight possible gap directions rather than four as in Experiment 1. Furthermore, to eliminate possible color-based priming from the test displays to the cue display on the subsequent trial, the test displays contained only black Landolt C's.

Results

Behavior

Figure 2b shows the average search RT and error rate for each task type and target repetition in Experiment 2. The main effect of task type on RT was significant, $F(1, 15) = 201.66$, $p < .001$, $\eta_p^2 = .93$. RT was lower in simple recognition task, than in the nondistinct target search task. Neither the main effect of repetition, $F(1, 15) = 3.04$, $p = .102$, $\eta_p^2 = .17$, nor the task type x repetition interaction was significant, $F(4, 60) = .12$, $p = .974$, $\eta_p^2 = .01$. The error rate pattern was similar to that of the RT. Participants were more accurate on simple recognition trials compared to nondistinct target search trials, $F(1, 15) = 105.27$, $p < .001$, $\eta_p^2 = .88$. Neither the main effect of repetition, $F(1, 15) = .88$, $p = .364$, $\eta_p^2 = .06$, nor the task type x repetition interaction was significant, $F(4, 60) = .86$, $p = .494$, $\eta_p^2 = .05$.

Electrophysiology

Figure 5 shows the CDA waveforms averaged across the electrode pairs used in the analyses (P5/6, P7/8, PO7/8 and O1/2). The main effect of contralaterality was significant, $F(1, 15) = 36.65$, $p < .001$, $\eta_p^2 = .71$, indicating that a CDA was triggered by the onset of the cue. This CDA decreased in amplitude with target repetition, as indicated by a contralaterality x repetition interaction, $F(1, 15) = 4.73$, $p = .046$, $\eta_p^2 = .24$. The CDA amplitude was again not different for both task types, as there was no task type x contralaterality interaction, $F(1, 15) = 2.50$, $p = .135$, $\eta_p^2 = .14$. Importantly, no difference was found in the overall rate of decrease of the CDA across task types, as suggested by the lack of a task type x contralaterality x repetition interaction, $F(1, 11) = .22$, $p = .643$, $\eta_p^2 = .02$. The contralaterality x electrode pair interaction was significant, $F(3, 45) = 4.31$, p

=.009, η_p^2= .23. SNK tests on CDA (contra- minus ipsilateral waves) showed that the CDA amplitude at PO7/8 (*M* = -0.93, *SD* = 0.72 µV), P7/8 (*M* = -0.85, *SD* = 0.55 µV), and P5/6 (*M* = -0.78, *SD* = 0.48 µV) were equal and all greater than at O1/2 (*M* = -0.61, *SD* = 0.51 µV). No other interaction was significant (all *F*s < 2.50, *p*s > .135). Consistent with the ANOVA, the Bayes Factor analysis indicated that the null hypothesis (no difference in CDA between task types) was 1.8 times more likely to be true than the alternative hypothesis (a CDA difference between task types), JZS Bayes Factor (null/alternative) = 1.8 (Rouder et al., 2009). For the contralaterality x task type x repetition, the null hypothesis (no difference in the rate of decrease in CDA across task types) was 3.4 times more likely than the alternative hypothesis (a difference in the rate of decrease in CDA across task types), JZS Bayes Factor (null/alternative) = 3.4 (Rouder et al., 2009).

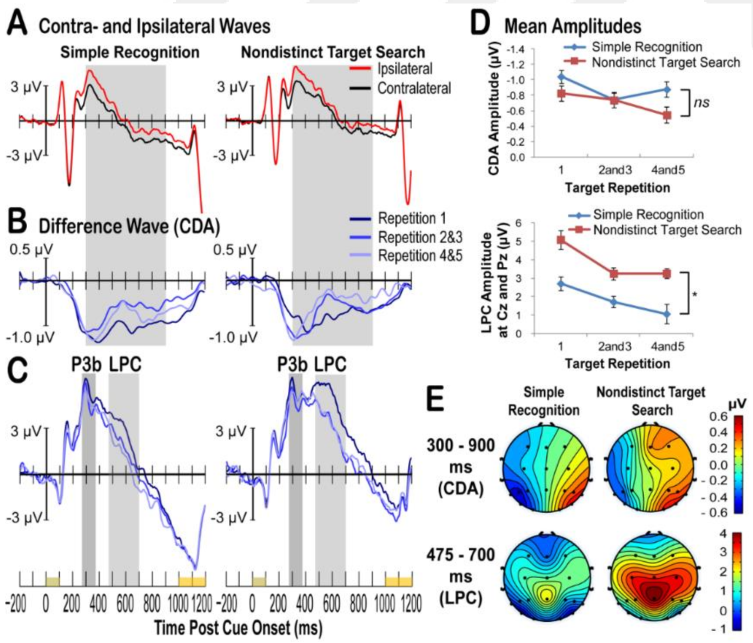

Figure 3.5. ERP results from Experiment 2. (a) The grand average waveforms at the average of PO7/8, P7/8, P5/6, and O1/2 electrodes, contralateral (black) and ipsilateral (red) to the location of the cue, plotted separately for simple recognition task (left panel) and nondistinct target search task (right panel). The gray rectangular region represent the time window at which CDA was calculated (300-900 ms). The shadings on the timeline indicate the duration of the cue (dark yellow) and search display (light yellow). Note that positive is plotted upwards. (b) The grand average waveform of CDA, and (c) The grand average waveform of P3b (275-375 ms) and LPC (475-700 ms), averaged across Cz and Pz, the electrodes where the LPC amplitude was largest, given separately across target repetitions shown in shades of blue. (d) Plots of grand average CDA and LPC amplitudes given separately for each task type and target repetition (shown in x-axis). The error bars represent standard errors of the mean for normalized data, i.e. corrected for between-subjects variance (Cousineau, 2005). (e) The scalp distribution of the CDA (top panel), and the LPC (bottom panel) calculated the same way as in Figure 3 (Experiment 1).

Figure 5 shows the LPC waves calculated at Cz and Pz. There was a main effect of electrode, $F(2, 30) = 5.82$, $p = .018$, $\eta_p^2 = .28$. SNK tests yielded that the LPC at Pz ($M = 3.30$, $SD = 2.87$ µV) and at Cz ($M = 2.41$, $SD = 3.13$ µV) were not different and were both greater than at Fz ($M = .91$, $SD = 3.09$ µV). There was an effect of target repetition, $F(1, 15) = 19.87$, $p < .001$, $\eta_p^2 = .57$. Like the CDA, the LPC amplitude decreased with target repetition. In contrast to the CDA, the main effect of task type was now also significant, $F(1, 15) = 9.18$, $p = .008$, $\eta_p^2 = .38$; the LPC amplitude was greater in nondistinct target task ($M = 3.11$, $SD = 3.12$ µV) than in change task ($M = 1.30$, $SD = 2.49$ µV). No interaction was significant (all *F*s < 2.14, *p*s > .14).

Figure 5 also shows the P3b waves calculated at Cz and Pz. There was a main effect of electrode on P3b amplitude, $F(1, 15) = 6.23$, $p = .016$, $\eta_p^2 = .29$. SNK tests yielded that P3b at Pz ($M = 5.83$, $SD = 3.13$ µV) was greater than both at Cz ($M = 4.27$, $SD = 3.86$ µV) and at Fz ($M = 3.43$, $SD = 3.38$ µV), which were not significantly different than each other. The P3b was not sensitive to task type, $F(1, 15) = 0.85$, $p = .775$, $\eta_p^2 = .01$. The electrode x task type was also not significant, $F(1, 15) = 0.40$, $p = .961$, $\eta_p^2 = .01$. There was a main effect of repetition on P3b amplitude, $F(1, 15) = 4.76$, $p = .045$, $\eta_p^2 = .24$. The P3b amplitude decreased with target repetition. No other interaction was significant (all *F*s < 2.44, *p*s > .14).

As seen in Figure 4, and confirmed by Pearson's product-moment correlation, the mean LPC amplitude calculated at Cz and Pz (the electrodes where its amplitude was largest) marginally correlated with mean RT in nondistinct target search task, $r(16) = .470$, $p = .066$. No other correlation was significant (*p*s>.194).

Discussion

Experiment 2 tested whether learning, as indicated by a decrease in VWM related components, occurs at a different rate for a search template in comparison to a VWM representation maintained for a simple recognition task. The CDA and LPC (and also the P3b) decreased at the same rate for each task, suggesting that the rate of learning, as well as the rate of decrease in the effort of maintenance, are equal for a VWM representation used for a search task and for a simple recognition task. The remaining results were consistent with Experiment 1; (1) responses were faster and more accurate in simple recognition compared to nondistinct target search task, (2) the LPC but not the CDA (nor the P3b), was sensitive to the task type, and (3) participants who invested less effort for maintaining the VWM representations, the 'efficient maintainers', performed faster, though only in the nondistinct search task.

General Discussion

By investigating two ERP components related to WM maintenance, the present study tested whether maintenance and learning of a VWM representation change as a function of whether this representation is stored to be used for visual search or for simple recognition. The behavioral results of both experiments showed that the search tasks were more effortful (i.e. participants were less rapid and less accurate) than a simple recognition task. In terms of ERPs, for both experiments, the LPC was greater in the search tasks compared to the simple recognition task. However, its scalp distribution did not change. Moreover, neither did the scalp distribution of the CDA nor its amplitude change across tasks, suggesting that the quality of a VWM representation does not depend on the upcoming task type. These results are in line with findings from Gunseli et al. (in press) and provide support for the claims made there that anticipating a difficult task leads to a greater working memory effort, reflected in a larger LPC, but that the quality of the representation, indexed by the CDA, is not sensitive to this anticipated task difficulty. The present study extends these findings by demonstrating that the CDA is also insensitive to the upcoming task for which the maintained representation is going to be used.

The rate of learning across target repetitions, that is, a decrease in VWM involvement for maintaining a representation (as expressed by declining CDA and LPC amplitudes) was also equal for search and simple recognition tasks (Experiment 2). The learning of a VWM representation has been observed before separately for visual search (Carlisle et al., 2011; Gunseli et al., in press; Reinhart et al., 2014b; Reinhart & Woodman, 2013) and simple recognition tasks (Reinhart & Woodman, 2013). In the present study, we replicated these findings and additionally showed that the rate of learning is equal for a search template maintained for search and a VWM representation maintained for simple recognition. This result extends our previous findings of equal learning rates across search tasks of varying difficulty (Gunseli et al., in press), and shows that the learning rate of a VWM representation is also independent of its functional role in the subsequent task.

Participants who invested less in maintaining a VWM representation (as indexed by smaller mean LPCs) performed faster in both tasks. This result is in line with results from Gunseli et al. (in press) that showed the same relationship for repeated search and extends it further to a simple recognition task. We propose that, since VWM has a limited capacity (Luck & Vogel, 1997; Vogel & Machizawa, 2004), if less VWM effort is invested in maintaining the cue, more resources can be devoted for performing the task itself. This, in turn, might lead to a faster performance. In line with this, previous research observed that participants who respond faster in a WM task has less BOLD activity in WM related brain regions (Rypma & D'Esposito, 2000), and that action video game players, who are known to have better quality VWM representations compared to non-gamers (Sungur &

Boduroglu, 2012), have reduced activity in fronto-parietal network (Bavelier, Achtman, Mani, & Föcker, 2012). Similarly, WM training, which leads to an increase in VWM capacity, has been observed to result in a reduced CDA amplitude, which was suggested to be due to improved efficiency in fronto-parietal network activation (Kundu, Sutterer, Emrich, & Postle, 2013). These results support the view that individuals who devote less effort for WM performance are actually the ones that are more efficient in performing this task. Moreover, it is noteworthy that the fronto-temporal network, which was suggested to underlie the improvement in WM efficiency in these studies, was also claimed to constitute the source of P3b/LPC formation (Polich, 2007; Polich, 2012). This would explain why the LPC amplitude was correlated with the behavioral performance in this and our previous study (Gunseli et al., in press). The lack of a similar effect on the CDA can be attributed to fact that there was only a single object to remember, and thus it was not possible to make maintenance more efficient quantitatively (consistent with Kundu et al., 2013, who observed a training-related CDA decrase, only at set size 4). An alternative but not necessarily mutually exclusive explanation for the LPC-RT correlation is that, as the representations are learned over the course of the experiment, both their reactivation in VWM, and also their identification in the test display might become less effortful, leading to smaller LPC and RTs.

A distinction has been made between 'privileged' representations in VWM that are in the focus of attention and other representations within WM referred to as the region of direct-access (Oberauer, 2002), or activated long-term memory (Cowan, 1995, 1999). Indeed, focusing attention to a particular representation in VWM has been suggested to result in functional and neurological changes in its maintenance (Kuo, Stokes, & Nobre, 2012; LaRocque, Lewis-Peacock, Drysdale, Oberauer, & Postle, 2013; for a review, see LaRocque et al., 2014; Lepsien & Nobre, 2007; Lewis-Peacock et al., 2012; Nee & Jonides, 2013; Nelissen, Stokes, Nobre, & Rushworth, 2013; Öztekin, Davachi, & McElree, 2010). Similarly, VWM representations that guide visual attention, i.e. search templates, have also been suggested to be prioritized by means of focused attention within VWM, relative to 'accessory WM items' that must be maintained for a later test but are not required for performing in the upcoming search task (Olivers & Eimer, 2011; for a review, see Olivers et al., 2011; Peters et al., 2009; Peters et al., 2012). In the present study, for all tasks, there was just a single representation to be maintained, which was presumably always in the focus of attention. Nevertheless, participants invested greater effort, as shown by a larger LPC, in maintaining this single representation when the upcoming task was anticipated to be more difficult. This result suggests that even within the focus of attention, which has been considered as a privileged unitary state of WM, representations can receive a graded amount of effort invested for their maintenance, depending on the difficulty of the upcoming task. Yet, it should be noted that our results do not, and cannot, argue against two states of WM, as we have not compared maintenance for currently relevant versus currently irrelevant (accessory) items.

The LPC, has been claimed index many different cognitive functions such as context update, arousal, or subjective visual awareness. We believe that, in the present procedure, the WM maintenance is the most plausible explanation that is also consistent with the literature. Another alternative explanation regarding the LPC sensitivity to upcoming task difficulty is the preparation for ignoring the distractors in the search task, which is more effortful in the nondistinct target search task. However, if this was the case, then the individuals that are overall better prepared, in other words, the ones with larger LPCs, should have responded faster. Conversely, we observed the opposite pattern, that is, a positive correlation between the LPC and RT for the nondistinct target search task in Experiment 2, arguing against this alternative explanation.

In line with earlier claims, we observed both similarities and differences between the P3b and the LPC. The LPC amplitude was greatest at both Cz and Pz, whereas the P3b amplitude was largest at Pz. Moreover, the P3b was either weakly sensitive (Experiment 1) or not sensitive at all (Experiment 2) to task type (see also Gunseli et al., in press, for a similar pattern), while the LPC was sensitive to task type in both experiments. On the other hand, P3b and the LPC were both sensitive to target repetitions (i.e. learning). The distinction between the P3b and the LPC is in line with the literature and suggests that, although they can have similarities, the P3b, defined as the narrow peak at central-parietal regions around 300 ms, does not always reflect the same cognitive processes as the LPC, which has a wider time range, a slightly different scalp topography, and can be sensitive to different experimental manipulations (Gunseli et al., in press; Kusak et al., 2000; Ruchkin et al., 1990; Ruchkin & Sutton, 1983; Sutton & Ruchkin, 2006).

In summary, we found that the effort invested in maintaining a VWM representation, as indexed by the LPC amplitude, is proportional to the difficulty of the upcoming task. Greater effort is invested in maintaining a VWM representation when it will be used for visual search, than when it will be used for simple recognition. However, neither the scalp distribution of the LPC nor any aspect of the CDA was affected by task type. The rate of learning a VWM representation, as indexed by the decrease in CDA and LPC amplitudes, was also not dependent on the upcoming task. Our results demonstrate that the functional role of VWM representations does not qualitatively change the underlying neural activity – at least not the activity reflected by the CDA and LPC. This suggests that a search template is not a special category of VWM representations, when compared to a representation used for a simple recognition task. A role in visual search does, however, affect the amount of working memory effort invested in the template's maintenance.

Chapter 4

Task-Irrelevant Memories Rapidly Gain Attentional Control with Learning

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Abstract

Although many of our perceptual biases stem from long-term, repeated exposure, current theories of visual search assume a central role for visual working memory (VWM) in guiding attention to target information. Crucially, whether a VWM representation guides attention depends on the relative priority that the memory has within VWM. Here, in a combined visual search/VWM task, we used attentional guidance by irrelevant memories to measure how long a target representation remain prioritized in VWM when observers repeatedly search for the same target. Irrelevant memories started guiding attention already when the target was repeated once, indicating that the target representation rapidly lost priority within VWM as it is moved to long term memory. By showing that training can lead to interference from irrelevant memories, the findings resolve a long-standing paradox on why VWM appears central to, yet at the same time not sufficient nor necessary for attentional guidance.

Introduction

We often search for visual objects such as a friend, a tennis ball, or a particular key on a keyboard. Most theories of attention claim that visual search requires a visual working memory (VWM) representation that acts like a “search template” or “attentional template” by specifying the target (Bundesen et al., 2005; Chelazzi et al., 1993; Desimone & Duncan, 1995; Wolfe et al., 1989). Consistent with this, some studies have found that maintaining a VWM is *sufficient* for guiding attention (Olivers et al., 2006; Soto et al., 2005). In these studies, participants performed a visual search task while also maintaining a VWM representation that was only relevant for a later task – the *accessory* memory item. Distractor objects that matched the accessory memory item interfered more with the search than unrelated distractors, even though both the distractor object and the accessory memory item were irrelevant to the search. However, other studies using variants of this paradigm failed to find interference from memory-matching distractors (Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006; Olivers, 2009; Woodman & Luck, 2007), suggesting that maintaining a VWM is actually not sufficient for guiding attention.

Moreover, recent EEG studies have provided evidence that VWM may not even be *necessary* for visual search (Carlisle et al., 2011; Gunseli et al., 2014a; Gunseli et al., 2014b; Reinhart et al., 2014a). These studies have shown a marked and rapid reduction in VWM related event-related potential (ERP) components when the search target is repeated, which suggests a handoff of the template from VWM to long term memory (LTM), consistent with theories of learning and automaticity (Anderson, 2000; Logan, 1988; Shiffrin & Schneider, 1977) and previous studies that have observed a role of long-term memory in guiding attention (Hutchinson & Turk-Browne, 2012; Olivers, 2011). In fact, one may argue that most of our everyday attentional biases stem from repeated exposure, and are engrained in LTM. The evidence that VWM is neither always necessary, nor always sufficient to guide attention is puzzling for theories that put VWM at the heart of attentional guidance.

One piece of this puzzle may be the current understanding that not all VWM representations are equal. There is converging evidence for a functional dissociation between a most relevant, prioritized, item and (at least momentarily) less relevant, non-prioritized items in VWM (LaRocque et al., 2014; Lewis-Peacock et al., 2012; Lewis-Peacock & Postle, 2012; McElree, 1998; Oberauer, 2002; Zokaei et al., 2014a). Specifically, attention has been suggested to be guided by the prioritized item in VWM, but not by non-prioritized items, which appear to be kept in a more passive state (Carlisle & Woodman, 2011a; Olivers & Eimer, 2011; for a review, see Olivers et al., 2011; Peters et al., 2009; Peters et al., 2012). It seems sensible to assume that when a template is represented in VWM, it will typically be in a prioritized state, reducing accessory items in VWM to the non-prioritized state in which they do not guide attention. Conversely, when the template is no longer that strongly represented in VWM, the accessory item gains priority, and as a result acquires an influence on attention. We hypothesize that this occurs when the target template is learned, and its representation is handed off to LTM.

Initial evidence for the role of learning in VWM-based guidance comes from the division between studies that did (Olivers et al., 2006; Olivers, 2009; Soto et al., 2005) and those that did not observe an influence of accessory memories on attention (Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006). In the first set of studies the target remained the same throughout the experiment, probably causing it to be well learned. Assuming such a well-learned template is no longer present in VWM, accessory items could gain prioritized status (but see Woodman & Luck, 2007). In contrast, in the second set of studies the search target was always new, probably resulting in a strong VWM presence that would prevent the accessory item from being prioritized. Consistent with this, Woodman, Luck, and Schall (2007) showed that visual search efficiency suffers from additional VWM load, but only for changing targets. When the target template remains constant, and thus presumably does not reside in VWM, it is not affected by other VWM items. Furthermore, Olivers (2009) found evidence for guidance from accessory items when the target was constant, but not when it was variable (see van Moorselaar et al., 2014, for an alternative explanation). However, in Olivers (2009) memory load was a potential confound across the two conditions: The consistent target condition contained only a single memory item – the accessory item – whereas the variable mapping condition had two memory items. Previous studies have shown that VWM-based guidance is compromised for two versus a single item in memory (van Moorselaar et al., 2014). Moreover, as Olivers (2009) only compared complete blocks of tens of trials, his study did not shed light onthe point and speed of transition at which accessory memories start to bias attention.

Here we provide direct evidence for the hypothesis that learning a template leads to its de-prioritization in VWM, allowing the task-irrelevant accessory item to become prioritized within VWM. Moreover, we provide evidence that this deprioritizartion of a learned template occurs very rapidly, within just a couple of trials. We used the search task illustrated in Figure 1. On each trial, participants were presented with two items to remember; a search target (a particular shape), and a color. The color became only relevant after the search (or in Experiment 2, was relevant on only 20% of the trials) when participants were asked to report the memorized color, and during search it was thus an accessory memory. The search display contained the target, and a colored distractor which matched the accessory memory item on 50% of the trials. Importantly, the search target was then repeated for a number of consecutive trials. If this causes the template to be handed off from VWM to LTM, this should inadvertently lead to the prioritization of the accessory item (i.e. the color representation) within VWM, as it is no longer competing with the target representation. This in turn should lead to a stronger interference from a memory matching distractor in the search display, leading to slower responses. Thus, our framework makes the counterintuitive but crucial prediction that learning the task-*relevant* item causes increasing interference from task-*irrelevant* (accessory) items. In other words, where previous studies have observed *improved* search performance as the target template is handed off from VWM to LTM (e.g. Carlisle et al., 2011), our hypothesis predicts that repeating targets leads to a *worsening* of performance when there is a distractor that matches the accessory memory, as the transition from VWM to LTM results in a change in attentional priorities within VWM. Moreover, our method provides a behavioral measure for how rapidly this change in VWM occurs.

Such a result would be of significant theoretical importance. First, it would demonstrate that the problems of necessity and sufficiency regarding the role of VWM in attentional guidance are actually related: A task-irrelevant VWM becomes sufficient for driving attention when VWM is no longer necessary for the task-relevant item. This further bridges conflicting findings in the literature. Second, it provides further support for the idea that there are multiple states within VWM, as the accessory item changes from being deprioritized to being prioritized. Third, such a result would point to a distinction between at least two partly independent, parallel routes of prioritization, both operational at the same time. One is based on LTM and is expressed by improved search for repeated targets when no memory-matching distractor is present. The other is VWM based, and in the present experimental design leads to a worse search performance when there is a memory-matching distractor. Where previous studies have faced the difficulty that VWM-based guidance and LTM-based guidance worked in the same direction, making it difficult to dissociate them, our design can tear them apart exactly because they result in opposite effects. Because of this, our design may yield a clear indication of when, over the course of a set of repetitions, a transition from VWM-based guidance to LTM-based guidance occurs.

Method

Participants

Thirty-three (age between 18-28, mean 20.9; 26 female) and 31 (age between 17-29, mean 21.1; 24 female) healthy volunteers participated in Experiment 1 and 2 respectively for course credit or for monetary compensation, after informed consent. The study was reviewed by the faculty's Ethical Committee and conducted in accordance with the Declaration of Helsinki. Thirty participants were planned for each experiment, and extra participants, with some reserve, were run in order to replace outliers. Two participants in Experiment 1 were excluded from analysis, one due to low performance (mean search RT = 1503 ms, and memory deviation = 28.6 degrees, both beyond 2.5 standard deviations from the grand average RT of 1025 ms, and deviation of 15.8 degrees), while the other was listening to music during the experiment, contrary to instructions. One participant in Experiment 2 was excluded due to low performance (i.e. chance level- 50% - search accuracy, a mean search RT of 1661 ms, and a memory deviation of 42.9 degrees, both beyond 2.5 standard deviations from the grand average RT of 977 ms, and deviation, 17.6 degrees).

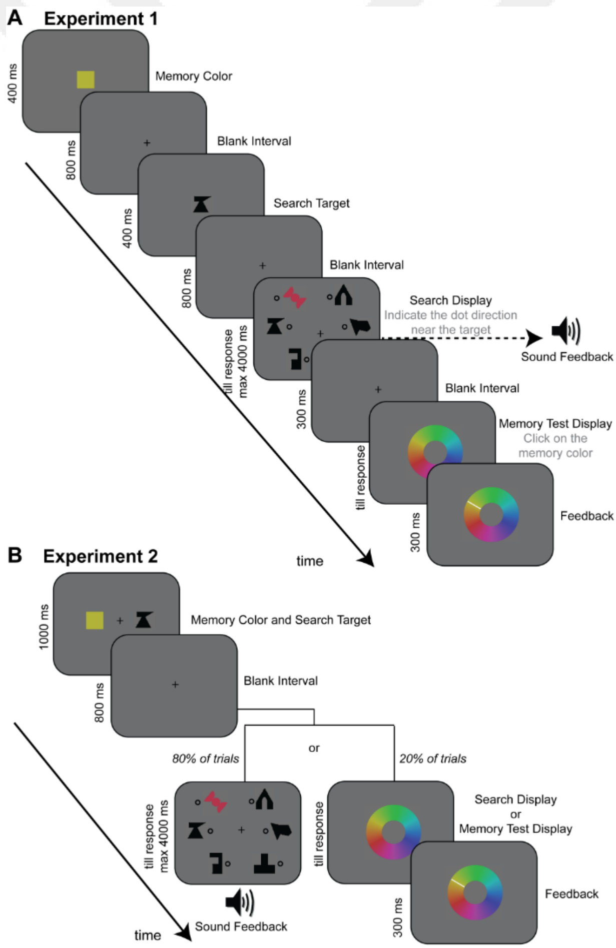

Figure 4.1. (a) The experimental procedure in Experiment 1. Participants were presented first with a memory color and then with a search target. After a blank period, they were presented with the search display. The task was to indicate the direction of the dot next to the target shape by pressing arrow keys (left vs. right). In this example, the correct response is 'right'. There was a colored distractor in the search display that matched the memory color on 50% of trials. In this example it is a memory-mismatching distractor color. After another blank interval, they received the memory test display. The task was to click on the memory color using the mouse. After the click, the position of the real memory color was shown with a white line. (b) The experimental procedure in Experiment 2 was the same except for the following. The memory color and the search target were presented simultaneously. After a blank interval, participants were presented either with the search display (80% of the trials) or the memory test display (20% of the trials).

Stimuli

All stimuli were presented on an LCD screen in a darkened cubicle. Viewing distance was approximately 75 cm. Figure 1 shows the sequence of events for both experiments. The background color was gray (15.64 Cd/m2). The fixation cross was a black plus sign (.20° of line length, .05°of line thickness) and was centrally presented (throughout the Method section we will use '°' to refer to the degrees of visual angle, and 'degrees' to refer to the circular distance on the color wheel). In Experiment 1, the search target and the memory color were presented sequentially at the center of the screen. In Experiment 2, they were simultaneously presented 1.02° of visual angle to the right and left of the center of the screen. The search target shape was always presented in black. The memory color was presented as a square (.50° x .50°). The search display consisted of multiple shapes (six or nine in Experiment 1, and always six in Experiment 2) presented on an imaginary circle with a radius of 3.82° in Experiment 1 and 3.18° in Experiment 2. In the search display, one shape was colored and the rest were black. There was also a dot (a small circle .08° of radius, .05° of line thickness) presented .13° to the left or right of each shape. The shapes were selected from a pool of 100 different shapes (1.42° x 1.42°) generated by Downing and Dodds (2004). The memory color was selected from a pool of 360 different color values that varied in hue, but had the same saturation (.7) and luminance (.7) values based on the HSL model. These color values were used to generate a ring (i.e. the color wheel) that was centrally presented during the memory test display, adopted from Hollingworth and Hwang (2013). The inner and outer radii of the color wheel were 3.82° and 8.89° respectively. The feedback for the search task was provided by two different tones indicating accuracy. The feedback for the memory task was a white line (.05° line thickness) extending from the inner radius to the outer radius of the color wheel overlaying the memory color.

Design and Procedure

Each trial started with the presentation of the fixation cross for a randomly jittered duration of 800-1000 ms. Then, in Experiment 1, the memory color was presented for 400 ms, followed by a blank interval of 800ms, and the presentation of the search target for 400 ms. After a second blank interval of 800 ms, the search display was presented until response or a maximum of 4000 ms. The task was to indicate the side of the dot next to the target shape using the arrow keys (i.e. left or right). Auditory feedback on accuracy was provided. Following another blank interval of 300 ms, the memory test display (i.e. the color wheel) was presented until participants mouse-clicked on the color wheel at the location of the memory color. Following a mouse response, the feedback line was presented for 300 ms.

The sequence of events in Experiment 2 was the same as Experiment 1 except for the following. The memory color and search target were presented simultaneously for 1000 ms. The side of the presentation of the search target and the memory color (i.e. left or right) was constant thorough the experimental session and was counterbalanced across participants. Following a blank interval of 800 ms, either a search display or the color wheel was presented. Task type was randomly distributed across trials with the constraint that 80% of trials per block would be a search task, and 20% a memory task. For both experiments, during the practice session, the search target and the memory color were presented 1000 ms longer than during the real session (in total, 1400 ms each in Experiment 1, and 2000 ms of simultaneous presentation in Experiment2).

Participants were told that each target was going to be repeated 20 a(Experiment 1) or 6 (Experiment 2) times in a row, and were also told that the colored shape in the search display was irrelevant for the task. They were asked to aim for speed without risking accuracy in the search task, and for precision (but not speed) in the memory task.

Experiment 1 employed a factorial design with 2 singleton types (memory-match; memory-mismatch), 2 set sizes (6; 9) and 20 repetitions. Singleton type, set size, and dot sides on the search display varied randomly. Experiment 2 employed a factorial design with 2 task types (search task; memory task), 2 singleton types (memory-match; memory-mismatch), and 6 repetitions; set size was constant (it was six) and the singleton type varied equally and randomly across trials per block.

Each experimental block contained 36 trials (x10 blocks) in Experiment 1, and 40 trials (x14 blocks) in Experiment 2. After each block, there was a self-paced break in which participants were presented with their cumulative average and block average search accuracy, search reaction time (RT), and deviation. At the beginning of each experimental session, participants performed a practice session of 16 trials in which they were required to achieve a search task accuracy of minimum 75% (80% for Experiment 2), and a memory task deviation of maximum 40 degrees (30 degrees for Experiment 2). Practice session was repeated until these requirements were achieved (1.4 and 1.8 blocks on average in Experiment 1 and Experiment 2 respectively).

For both experiments, a search target shape was not repeated as a target again during the experimental session once its repetition run was over, during a next repetition run, a search target shape from the previous repetition run was not used as a distractor shape, the target color in two consecutive trials were at least 45 degrees away on the color wheel, target color and the distractor color on every trial were at least 45 degrees away on the color wheel, on two consecutive trials, the location of the target (and also the distractor) on the search display was different, and the color wheel was randomly rotated 0, 60, 120, 180, 240, or 300 degrees on every trial.

Data Analysis

Where necessary, p-values were adjusted based on the Greenhouse–Geisser epsilon correction on degrees of freedom for sphericity violations (Jennings & Wood, 1976). The first trial of each block was excluded from the analysis. Results of statistical tests in terms of reaching significance were the same without this exclusion. In Experiment 1, consecutive repetitions were binned together to increase power (e.g. 1 and 2, 3 and 4, etc.).

Search task

The mean RT for each condition was calculated after the exclusion of the trials with incorrect responses in the search task, trials with a deviation larger than or equal to 45 degrees on the memory task (for Experiment 1 only), and outlier trials. Outlier trial removal was performed in two steps. First, trials with a search RT below 350 ms were rejected (0.24% and 0.14% of all trials for Experiment 1 and 2). The second step was a so-called non-recursive moving criterion procedure, in which trials were removed if the search RTs were beyond *s* standard deviations from the mean per condition, with *s* varying according to the number of data points in that condition (Van Selst & Jolicoeur, 1994). This procedure was preferred over a fixed cutoff point procedure because of the low number of trials per repetition condition in Experiment 1. This two-step trimming led to rejection of 2.82% and 3.01% of all trials in Experiment1 and 2. Accuracy analysis were performed on the trials that were trimmed based on search RT and memory deviation as described above.

Accuracy and RT were entered in separate repeated measures ANOVAs with the factors singleton type, target repetition and set size.[3] In order to test whether there is an involuntary attentional guidance by the memory color on each repetition, following a significant singleton type x repetition interaction, paired-sample t-tests were used to compare RTs across singleton types on each repetition. In order to test whether the size of involuntary attentional guidance by the memory color was different in early repetitions relative to the later repetitions, paired-sample t-tests were used to compare the *memory-driven interference* (i.e. the RT difference between memory-match and memory-mismatch trials) for each repetition against the mean of all further repetitions (i.e., 1 against the average of repetitions 2, 3, 4,…).

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[3] Data was collapsed across set size (except for set size analysis) because there was one participant who had no trials with a correct response in one bin in one condition.

Memory task

For each condition, the mean deviation score on the color memory test was calculated as the average deviation (i.e. error) of the color selected by the participant from the original memory color, in terms of angular degrees on the color wheel. In Experiment 1, the deviation analysis included trials with a correct search response only. Deviation scores were entered in a repeated measures ANOVA with the factors singleton type (only in Experiment 1), and target repetition (for both experiments). Singleton type was not defined for memory task trials in Experiment 2, because in this experiment a memory task never followed a search task. In Experiment 1, following a significant singleton type x repetition interaction, separate repeated measures ANOVAs were used for each singleton type with the target repetition. In order to infer whether the deviation decreased across target repetitions (i.e. memory performance increased), the effect of repetition was treated as a linear contrast (Rosenthal & Rosnow, 1985), but the results of the standard omnibus tests were the same (in terms of reaching significance).

Results

Experiment 1

Search RT

The mean RT in each condition is shown in Figure 2 (collapsed across set size). Responses were overall faster in memory-mismatch than on the memory-match trials, $F(1, 30) = 45.92$, $p<.001$, $\eta_p^2 = .60$ (main effect of singleton type), and they were also different across repetition bins, $F(5.45, 166.38) = 2.12$, $p = .058$, $\eta_p^2 = .07$. Importantly, these two factors interacted, $F(6.19, 185.77) = 2.16$, $p=.047$, $\eta_p^2 = .07$. RT on memory-match trials was larger than on memory-mismatch trials for each repetition bin (ts> 2.14, ps< .041), except bin 1, $t(30) = .63$, $p= .533$. Set size had a main effect on RT, $F(1, 29) = 256.62$, $p<.001$, $\eta_p^2 = .90$, Responses were overall slower for set size 9 (M= 1093.7 ms, SD= 182.0) compared to set size 6 (M= 905.7 ms, SD= 147.6).As it did not interact with other factors (Fs <1.68, p>.205), it is not reported on further.

Memory-driven interference, measured as the RT difference between memory-match and memory-mismatch distractor trials, is presented below the main panels of Figure 2. Interference was smaller in repetition bin 1 relative to the average of any of the other repetition bins (i.e. 2 to 10), $t(30) = 3.14$, $p= .004$; no further increase was seen from the second bin onwards (ts< .86, ps> .394).

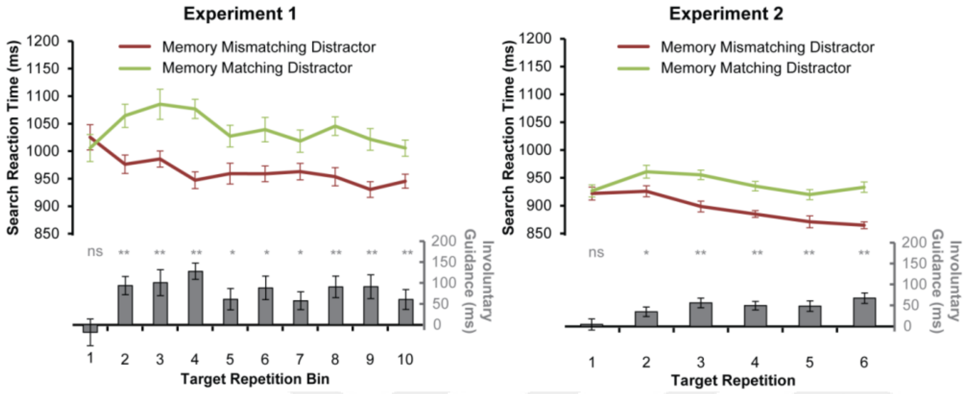

Figure 4.2. Search RT results from both experiments. Memory-mismatching and memory-matching distractor trials are shown in different colors, given in the legend. The column bars in the bottom panels show the RT difference between memory-match and memory-mismatch distractor trials (i.e. the memory-driven interference). The error bars represent standard mean errors for standardized data (i.e. corrected for between-subjects variance, Cousineau, 2005). The ns, '*' and '**' represent p> .05, p < .05 and p < .005 respectively, for t-tests comparing RT in memory-match and memory-mismatch trials (two-tailed).

Search accuracy

The mean accuracy for each condition is shown in Table 1. There was no main effect of singleton type, $F(1, 30) = .10$, $p = .748$, $\eta_p^2 = .01$, nor repetition bin on accuracy, $F(9, 270) = .691$, $p = .717$, $\eta_p^2 = .02$. There was a marginal singleton type x repetition bin interaction, $F(5.44, 163.09) = 1.86$, $p = .099$, $\eta_p^2 = .06$, which was not analyzed further as the pattern was not indicative of a speed-accuracy tradeoff. Set size had no effects on accuracy, *Fs*< 2.76, *ps* > .107.

Table 4.1. Search accuracies for both experiments given separately for each condition.

Accuracy (%)

					Experiment 1					
Target Repetition Bin	1	2	3	4	5	6	7	8	9	10
Memory-Match	98.5	97.3	97.1	97.4	97.0	97.4	96.7	97.2	97.4	97.9
Memory-Mismatch	96.2	96.6	97.3	98.1	96.3	97.6	98.9	98.1	98.4	98.1
					Experiment 2					
Target Repetition	1	2	3	4	5	6				
Memory-Match	95.1	97.5	96.7	96.8	97.3	96.2				
Memory-Mismatch	93.8	95.9	96.8	96.9	97.7	97.1				

Memory deviation

The mean deviation in each condition is shown in Figure 3. Deviation was smaller after memory-matching distractors than after memory mismatching distractors (main effect of singleton type), $F(1, 30) = 14.95$, $p<.001$, $\eta_p^2 = .33$, and there was a main effect of repetition bin on deviation, $(1, 30) = 6.08$, $p=.020$, $\eta_p^2 = .17$, and an interaction between these two factors, $(1, 30) = 6.25$, $p=.018$, $\eta_p^2 = .17$. Separate ANOVAs for each singleton type with bin as a linear factor showed that the deviation decreased with increasing repetitions for memory-match trials, $(1, 30) = 17.04$, $p<.001$, $\eta_p^2 = .36$, but not for memory-mismatch trials, $(1, 30) = .66$, $p=.799$, $\eta_p^2 = .01$.

Experiment 2

Experiment 1 showed that the size of involuntary guidance towards the color increased with repeated search for the same target. This result suggests that learning a template leads to its de-prioritization in VWM and consequently a prioritization of the accessory item. However, there is an alternative explanation. Participants might be voluntarily attending to the memory-matching color during search in order to refresh its memory representation for the upcoming memory task. In order to eliminate this alternative explanation, in Experiment 2 a memory task never followed a search task. Instead, at a given trial, participants either received the search or the memory task. Therefore, there was no benefit to deliberately attending to the distractor in the visual search task. Furthermore in Experiment 2, the memory task was not susceptible to any potential confounding effects of an intervening search task such as interference from a colored distractor or the re-prioritization of the target shape upon its detection.

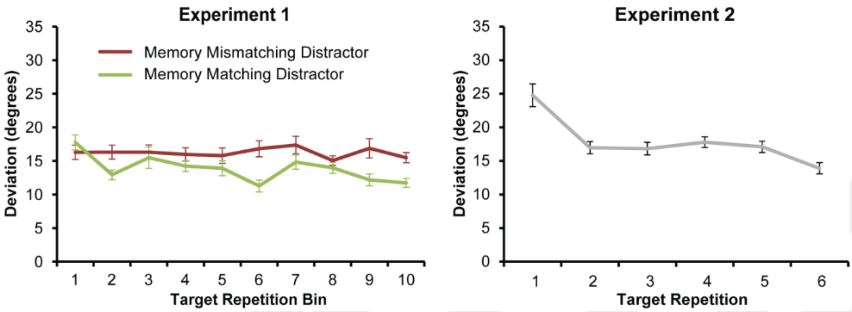

Figure 4.3. Memory deviation results from both experiments. Lower deviation values indicate better memory. Memory-mismatching and memory-matching distractor trials are shown in different colors, given in the legend. Note that in Experiment 2, the memory task never followed the search task, thus singleton type was thus not defined for memory task trials in Experiment 2. The error bars represent standard mean errors for standardized data (i.e. corrected for between-subjects variance, Cousineau, 2005).

Search RT

The average RT in each condition is shown in Figure 2, panel. Responses were overall faster in memory-mismatch than in memory-match trials, $F(1, 28) = 43.36$, $p<.001$, $\eta_p^2= .61$, and were different across repetitions, $F(5, 140) = 6.76$, $p<.001$, $\eta_p^2= .20$. As in Experiment 1, there was a singleton type x repetition interaction, $F(5, 140) = 2.76$, $p=.021$, $\eta_p^2= .09$: The RT on memory-match trials was larger than on memory-mismatch for each repetition (*ts* > 2.53, *ps* < .017), except the first one, $t(28) = .30$, $p = .766$.

Memory-driven interference, as measured through the RT difference between memory-match and memory-mismatch distractor trials, is also presented in Figure 2. Interference was smaller in repetition 1 relative to the average of other repetitions (i.e. 2 to 6), $t(28) = 2.93$, $p= .007$, but no further difference was seen from repetition 2 to 6 (i.e., interference on repetition 2 was not different from the mean of repetition 3 to 6, etc.; *ts*< 1.43, *ps*> .163).

Search accuracy

Mean accuracy in each condition is reported in Table 1. There was a main effect of repetition bin on accuracy that was not further explored, $F(2.80, 78.31) = 5.86$, $p =.001$, $\eta_p^2= .17$, but none of singleton type, $F(1, 28) = .58$, $p = .452$, $\eta_p^2= .02$, and no singleton type x repetition interaction, $F(5, 140) = 1.43$, $p=.217$, $\eta_p^2= .05$.

Memory deviation

The average deviation across repetitions is shown in Figure 3. There was a main effect of repetition on deviation, $F(1, 28) = 18.95$, $p<.001$, $\eta_p^2 = .40$, suggesting that the deviation decreased across target repetitions.

Discussion

Both experiments showed that repeating the search target led to improved search performance (expressed in decreasing RTs) as long as there was no memory-matching distractor present. In other words, the search target was effectively learned within a few trials, consistent with earlier work (e.g. Carlisle et al., 2011). Importantly, both experiments showed that learning the search target additionally makes *other* WM representations, though irrelevant for the search task, guide attention. Whenever observers encountered a new search target, memory-matching distractors did not interfere with search. However, interference rapidly emerged when participants searched for the same target again on subsequent trials. Moreover, recall performance for the memory item improved with repetition of the search target. Together these results suggest that, with learning the task-relevant stimulus, the relative attentional priorities within VWM rapidly change, as the VWM involvement for maintaining a search template reduces, and an irrelevant VWM representation inadvertently gains priority. Furthermore, the results suggest that this occurs already after one repetition, suggesting that a single experience with a search target is sufficient for at least a partial hand-off to other memory systems.

The results bridge the divide between studies that had a new target defined on every trial and failed to find attentional guidance from additional VWM content, and those that had a consistent target definition throughout the experiment and did find guidance from VWM (Downing & Dodds, 2004; Houtkamp & Roelfsema, 2006; Olivers et al., 2006; Olivers, 2009; Soto et al., 2005). Our data reveal the concurrent transition of i) the task-relevant item transferring from VWM to LTM, and ii) a task-irrelevant item transferring from a non-prioritized state (in which it does not guide attention) to a prioritized state (in which it does guide attention). Thus, our results show how learning a target unites the different claims in the literature regarding memory-driven interference. Our results also support the claim that multiple representations active in VWM influence attention less than a single active VWM representation (Olivers et al., 2011; van Moorselaar et al., 2014) by showing an increased VWM-based guidance as one of the two VWM representations is transferred to LTM.

Although our results provide an explanation for many inconsistent findings in the literature, there are some studies whose findings cannot be explained by target repetition alone (e.g. Carlisle & Woodman, 2011b; Woodman & Luck, 2007). These studies have used consistent targets yet failed to observe VWM driven involuntary attentional guidance This suggests that there may be other constraints on guidance by VWM representations that contributing to the inconsistent findings, such as perceptual difficulty of the search display (Han & Kim, 2009). However, our results clearly show that, when these constraints are met, learning the task-relevant VWM item makes a task-irrelevant VWM item involuntarily guide attention.

Our results are consistent with the idea that VWM comprises multiple states, such that only currently task-relevant items are maintained in a prioritized state characterized by neural activation, while currently irrelevant items are maintained in a more passive state (LaRocque et al., 2014; Lewis-Peacock et al., 2012; Lewis-Peacock & Postle, 2012; McElree, 1998; Oberauer, 2002; Olivers et al., 2011; Peters et al., 2012; Zokaei et al., 2014a). Our data show that a VWM can be prioritized in two ways: Either when it is a new template for the current task, or when it is an accessory item but the current task-relevant template is no longer represented in VWM (but presumably stored in LTM). In the latter case the accessory item, as the only one remaining, automatically gains priority. The fact that the prioritization of the accessory VWM item occurs even though it is detrimental for the task suggests that people may have imperfect control over the state of VWM items. Note the similarity to Lavie's perceptual load theory of attention, which states that available attentional resources for perception must be spent even if this leads to attending to distractors (e.g. Lavie, 1995). Here we suggest that this idea may generalize to the VWM domain by showing that resources available for mnemonic prioritization (or internal attention as some refer to it; Chun, 2011; Chun, Golomb, & Turk-Browne, 2011) are spent on the single item in VWM even if that item is task-irrelevant. In other words, if representations are being held in VWM, one of them will be in the prioritized state.

The results also provide direct evidence for two at least partly independent routes of top-down guidance of attention (Hutchinson & Turk-Browne, 2012): One route operates through prioritized VWM representations that guide attention (which may occur even when these are not task-relevant), while the other route goes via long-term memory representations of the search target. Because these two routes had opposite effects in our experiments, with repeated targets leading to faster baseline search but more VWM-based interference, our results provide particularly strong evidence for such dual routes to guidance. Interestingly, while normally VWM is seen as the gatekeeper for currently task-relevant activity protecting it against interference from task-irrelevant events (Corbetta & Shulman, 2002; Luck & Vogel, 2013; Schwager & Hagendorf, 2009; Zelinsky & Bisley, 2015), here we report the reverse case: The task-relevant representation drives attention from LTM, whereas the task-irrelevant representation stored in VWM causes interference. Thus, this finding argues against the assumption that VWM content implements current task goals.

The emergence of involuntary guidance from VWM was surprisingly rapid. Already at the second presentation of the same search target, the memory item started to cause interference. This is consistent with electrophysiological studies that investigated the markers of VWM maintenance of a template and observed the largest reduction in VWM involvement at the second target repetition (Carlisle et al., 2011; Gunseli et al., 2014a; Gunseli et al., 2014b; Reinhart et al., 2014a). However, although the decline was rapid, such electrophysiological markers of VWM did not completely disappear, and certainly not already at the second repetition, while in our studies involuntary guidance emerged with the second repetition and remained rather constant from thereon. There are two possible explanations. First, a complete handoff of the template from VWM may not be necessary for accessory items to start guiding attention. Instead, a mere reduction in VWM involvement for maintaining the template may be sufficient for accessory items to gain influence. Second, the handoff might be faster when there are competing demands on VWM (i.e., multiple representations for multiple tasks), as in the present study, than when compared to the electrophysiological studies in which there was less of a demand on VWM (i.e., a single representation for a single task). In any case, our results show that within a handful number of trials, observers go on autopilot, where their search is driven by long-term memories, and their VWM is driven by task-irrelevant objects.

Author Contributions

E.G., C.N.L.O., and M.M. designed the experiment, E.G. performed the experiment and analyzed the data, E.G., C.N.L.O., and M.M. wrote the manuscript.

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PART 2

ATTENTION TO MEMORY

Chapter 5

The Reliability of Retro-Cues Determines the Fate of Non-cued Visual Working Memory Representations

Gunseli, E., van Moorselaar, D., Meeter, M., & Olivers, C. N. (2015). The reliability of retro-cues determines the fate of noncued visual working memory representations. *Psychonomic Bulletin and Review*.

Abstract

Retrospectively cueing an item retained in visual working memory during maintenance is known to improve its retention. However, studies have provided conflicting results regarding the costs of such retro-cues for the non-cued items, leading to different theories on the mechanisms behind visual working memory maintenance and retro-cueing. Here we tested an alternative explanation of the conflicting results regarding retro-cue costs, namely that they are at least partly caused by differences in retro-cue reliability. We manipulated the ratio of valid cue trials to invalid cue trials within blocks. We used a continuous report procedure that allowed fitting a model that provided recall probability and precision estimates for memory representations. Reconciling previous contradictory findings, benefits for valid cues were observed in all conditions, but invalid cueing costs were found only when the retro-cue had a high reliability (i.e., was 80% valid) but not when it had a lower reliability (i.e., 50% valid). This was found for both the recall probability and the precision of visual working memory representations. Our results suggest that the cognitive mechanisms underlying retro-cue effects are strategically adjusted by participants depending on perceived retro-cue reliability.

Introduction

Visual working memory (VWM) is the cognitive system in which a limited amount of visual information can be briefly maintained and manipulated. Attention interacts with many stages of VWM processing, including encoding (Posner, 1980; Schmidt, Vogel, Woodman, & Luck, 2002; Vogel, Luck, & Shapiro, 1998), maintenance (Awh & Jonides, 2001; Awh, Jonides, & Reuter-Lorenz, 1998; Munneke, Heslenfeld, & Theeuwes, 2010), and retrieval (Theeuwes, Kramer, & Irwin, 2011). One way to look at this interaction is through the use of retro-cues. These are typically spatial cues presented during maintenance that point out one of the memory items, which then becomes particularly likely to be tested. It has been shown that such retro-cues result in improved memory performance compared to trials without a retro-cue (Griffin & Nobre, 2003; Landman et al., 2003; Lepsien et al., 2005). This retro-cue benefit has been claimed to reflect (a) the reallocation of attentional resources within memory, resulting in the protection of the cued representation against decay and interference (Protection Hypothesis, Makovski & Jiang, 2007; Makovski et al., 2008; Matsukura et al., 2007; Pertzov et al., 2013; van Moorselaar, Gunseli, Theeuwes, & Olivers, under review-a), (b) removing non-cued items from memory, therefore presumably reducing the inter-item interference and competition for resources (Removal Hypothesis, Kuo et al., 2012; Souza, Rerko, & Oberauer, 2014; Williams & Woodman, 2012), (c) carrying the cued item to a more robust or 'prioritized' state during maintenance without altering non-cued items (Prioritization During Maintenance, Myers et al., 2014; Rerko & Oberauer, 2013; Souza et al., 2014), or (d) prioritize the cued representation during retrieval without affecting maintenance per se (Prioritization During Retrieval, Astle et al., 2012; Nobre, Griffin, & Rao, 2007).

Although all these hypotheses predict a benefit for the cued representation, they differ in their assumptions regarding the costs for non-cued representations. The Protection and Removal hypotheses predict that retro-cueing benefits for the cued representation should be accompanied by costs for non-cued representations because they involve reallocation of resources away from non-cued items towards the cued one. The Prioritization During Maintenance and Prioritization During Retrieval hypotheses, on the other hand, predict no such costs because they explain the cue benefits by a change in the *status* of the cued item without any change for non-cued items. Previous studies using retro-cues have so far produced conflicting results. Some have observed costs in recognition or recall performance when a non-cued representation is probed (Matsukura et al., 2007; Pertzov et al., 2013), while others have observed no such costs in these so-called *invalid trials* (Landman et al., 2003; Lepsien & Nobre, 2007; Rerko & Oberauer, 2013). The studies that did not observe any invalidity costs used a double-cueing paradigm in which an invalid cue is followed by a valid cue. This may make participants more hesitant to drop an item after the first cue. However, Matsukura et al. (2007)

observed a cost of invalid retro-cueing while using a double-cueing paradigm. Therefore, we believe double-cueing itself cannot account for the inconsistency across findings regarding invalidity costs. Yet again, other studies have observed costs only in reaction time and not accuracy, which has been interpreted as support for the Prioritization During Retrieval hypothesis (Astle et al., 2012). The lack of costs for non-cued items in recognition accuracy has gained further theoretical significance because it has been taken as evidence for the idea that VWM maintenance does not require any active rehearsal via attention (for a similar argument, see Hollingworth & Maxcey-Richard, 2013; Rerko & Oberauer, 2013). Thus, knowing whether retro-cues result in costs for non-cued representations is theoretically important for understanding the mechanisms behind VWM maintenance, as well as those behind retro-cueing.

Although we cannot nor wish to exclude the possibility of different factors playing a role, the present study investigated a factor that may at least partially explain the inconsistency in cue-related costs, namely the reliability of the cue. A similar argument has been made by Williams and Woodman (2012) in the context of directed forgetting cues. Cue reliability can be operationally defined as the ratio between valid and invalid trials.[4] Typically, studies that failed to observe a cost in invalid trials had relatively low cue reliabilities (50% valid, Landman et al., 2003; 50% valid, Lepsien & Nobre, 2007; 66.6% valid, Rerko & Oberauer, 2013) than those that observed a cost (80% valid, Astle et al., 2012; 75% valid, Matsukura et al., 2007; 70% valid, Pertzov et al., 2013). It may thus be the case that when a cue has a high reliability (e.g. a high valid to invalid trial ratio), participants devote most of their attentional resources to the cued representation (i.e. Protection) and remove the non-cued items from memory (i.e. Removal) since there is very little chance of being tested on them. On the other hand, when a cue has a low reliability (e.g. a low valid to invalid trial ratio), participants may keep on maintaining non-cued representations in anticipation of potentially being tested on them. In this case, they may merely prioritize the cued item during maintenance and/or retrieval, without costs to the non-cued representations. This straightforward hypothesis might account for the inconsistencies in the literature regarding the costs of invalid retro-cues.

We tested the cue reliability hypothesis by manipulating the validity of the retro-cue. Participants were asked to remember orientations of four bars and then recall the orientation of one probe bar. On some trials, during the maintenance interval a probabilistic retro-cue was presented: It pointed to the subsequently probed item in 80% of trials on some blocks (80% validity), and in 50% of trials on other blocks (50% validity).

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[4] Note that some studies defined validity ratios calculated as the number of trials $^{valid}/_{(valid+neutral+invalid)}$ instead of $^{valid}/_{(valid+invalid)}$. In the present study we used the latter since we did not expect trials without a cue to affect the subjective evaluation of the reliability of the cue.

On the remaining, invalid trials it pointed to one of the items that was *not* subsequently probed. Participants were informed about these validity ratios before each block. Furthermore, rather than employing the often-used change detection / recognition task, in which observers can only provide a discrete same/different judgment, we used a continuous-recall procedure that provides a more sensitive measure of maintenance of VWM representations that provides a degree of quality of recall performance, rather than reducing it to a binary decision (Bays, Catalao, & Husain, 2009; Wilken & Ma, 2004; Zhang & Luck, 2008). This measure also enabled fitting a model that estimates the recall probability of the target, non-target (i.e. non-probed) representations, and also the precision of memory. To foreshadow the main findings, retro-cues improved the recall probability and precision of the target. Importantly, both the benefits of valid retro-cues and the costs of invalid retro-cues were greater when the cue was highly reliable (i.e. 80% valid in comparison to 50% valid), to the extent that an invalidity cost was absent for probability and precision in the low reliability condition.

Method

Experimental Procedures

Twenty-two healthy volunteers participated in the experiment for course credit or monetary compensation. For twelve of the participants, we also took EEG recordings for another study. Their behavioral performance was no different from the rest. Two participants were excluded from analysis due to low performance (see Analysis). The study was conducted in accordance with the Declaration of Helsinki and was approved by the faculty's Ethical Committee. Written informed consent was obtained.

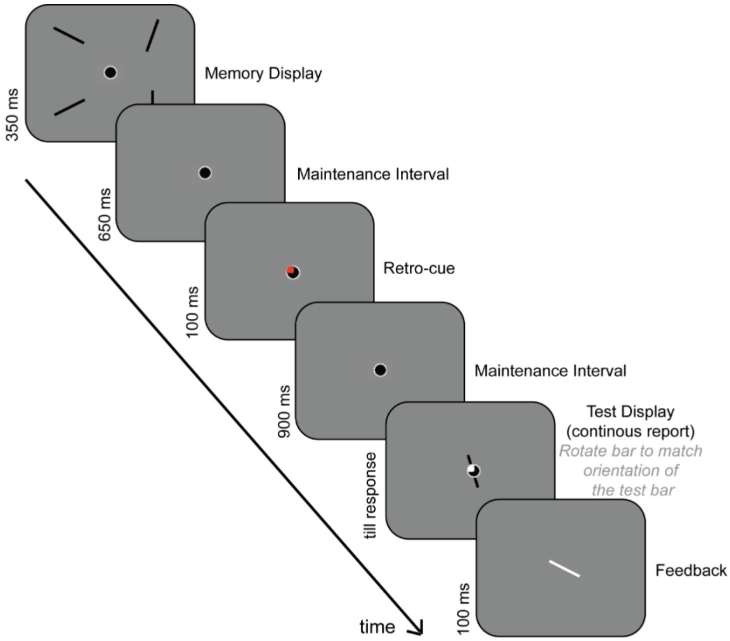

Figure 5.1. The experimental procedure in the present experiment. The retro-cue was a fixation circle with a quarter filled with either red or green to point one of the memory representations. Similarly, the test probe was indicated by a white quarter filling. In this example, participants needed to report the orientation of the bar presented on bottom-right corner, and the retro-cue is valid since it pointed in the same position. There were also trials in which the retro-cue was invalidly pointing to a bar that was not going to be tested. In neutral (i.e. no-cue) trials, the fixation dot remained on the screen during the retro-cue duration. During test, participants had to rotate the orientation of the bar to match that in their memory using the mouse.

The procedure is shown in Figure 1. The memory display consisted of four black oriented bars (2.08º x 0.25º visual angle) located equidistantly on an imaginary circle of radius 3.50º, and was presented for 350 ms. The orientation of each bar was chosen at random with the restriction that bars within the same trial differed by at least 10º. The test display was presented 1550 ms after the offset of the memory display (1650 ms for the 12 participants for whom the EEG was also recorded). It contained a randomly oriented bar and a cue pointing to the location of the probe representation that were both presented at the center of the screen. This probe cue was the same as the fixation circle except that a quarter (90º) of it was filled white. Participants were asked to indicate the precise orientation of the bar at the probed location by rotating the probe bar using the mouse. After a mouse response was made, the correct orientation was indicated by a central white bar for 100 ms. The inter-trial interval was 800 ms for ten participants, and a jittered interval between 1200-1600 ms for the other twelve.

On retro-cue trials, after the memory display, there was a maintenance interval of either 550 ms (for ten participants) or 650 ms (for 12 participants), followed by the presentation of the retro-cue display for 100 ms. The retro-cue was the same as the probe cue except the fill color was either red, 27.08 Cd/m^2, or green, 24.10 Cd/m^2, depending on the reliability condition (order counterbalanced). For the initial practice phase where the cue was 100% valid, the retro-cue fill color was orange (53.46 Cd/m^2). Following the retro-cue, there was a second maintenance interval of 900 ms. In no-cue trials, the black fixation circle remained on the screen during the whole maintenance interval without any changes to it. The timing of the test display was matched for retro-cue and no-cue trials.

In the high reliability condition, the cue was 80% valid and in the low reliability condition it was 50% valid. The reliability conditions were blocked. In each experimental block, 25% of the trials were neutral - that is, there was no cue. Each validity condition (i.e. valid, neutral, and invalid) was randomly intermixed within each block. Before each reliability condition, participants were informed about the validity ratio of the cues (as was also indicated by the color of the cue), and they performed a practice session of 25 trials to get used to this particular validity ratio. Moreover, at the beginning of the experiment, there was an initial practice session with a 100% valid cue that contained 20 trials (25 for 12 of the participants), to make participants familiar with the cue. In total, there were 560 trials (600 for 12 of the participants). In order to have a reasonable number of invalid cue trials, there were more blocks of the high reliable cue condition than of the low reliable cue condition. Respectively for valid, neutral, and invalid trials, there were 216, 90, and 54 trials for 80% valid cue, and 75, 75, and 50 trials (90, 90, and 60 for 12 of the participants) for 50% valid cue. The main constraint was to have at least 50 trials per condition for a reliable model fit (see, http://www.paulbays.com/code/JV10/index.php). At the end of each block, participants received feedback on block average and grand average memory deviation values.

Analysis

Deviation scores on the memory test were calculated as the average difference (i.e. error) between the original orientation of the probed memory bar and the orientation of the response. The precision was calculated, per condition, as the inverse of the standard deviation of the error in subjects' responses (Bays et al., 2009). The deviation scores were entered into a model to calculate the probability of recall for the target and non-target VWM representations (Bays et al., 2009). Two participants were excluded from further analysis due to low performance: one had a target recall probability barely above chance level (i.e. above the chance of reporting any of the four orientations) in the 50% valid no-cue condition (a fitted recall probability of .26 and an average deviation of 37.1 degrees), and the other had a recall probability of .51 (and an average deviation of 34.8) in 80%

valid no-cue condition that was almost the same probability of reporting one of the non-probed items (i.e. .49). Moreover, these target recall probabilities were 2.5 times the standard deviation lower than the overall mean for the given condition. The important results were the same when these participants were included. Raw deviation, target recall probability, non-target recall probability and precision for each condition were entered into a repeated-measures ANOVA with the factors of reliability (80% valid vs. 50% valid) and validity (valid, neutral, and invalid). Contingent on a significant reliability x validity interaction, these were followed up by separate ANOVAs testing for validity benefits (i.e. the difference between neutral and valid trials) and invalidity costs (i.e. the difference between invalid and neutral trials). Where necessary, p-values were adjusted for sphericity violations using the Greenhouse–Geisser epsilon correction on degrees of freedom (Jennings & Wood, 1976). To test whether the validity benefits and invalidity costs were different than zero, one-sample t-tests were used.

Results

We first tested whether the two reliability conditions differed in how participants performed on neutral trials. Any differences on neutral trials would have suggested that altering cue reliability would have changed the way participants approached the whole task. For all measures described below (i.e. raw deviation, precision, recall probability for the target, and the recall probability for the non-target), the performance on neutral trials did not differ between 80% valid and 50% valid conditions (all ts <1.00, ps>.330).

Raw Deviation

Next, we looked at the effect of cue validity and reliability on raw deviations from the target orientation. Figure 2A shows the distribution of errors for each condition, at which each data point represents the frequency of errors for bins of 15 degrees of deviations (Pertzov & Husain, 2013). There was no main effect of reliability on deviation, $F(1, 19) = 2.10$, $p = .163$, $\eta_p^2 = .10$, but there was one of validity, $F(2, 38) = 10.23$, $p < .001$, $\eta_p^2 = .35$. Importantly, there was a reliability x validity interaction, $F(2, 38) = 26.15$, $p < .001$, $\eta_p^2 = .58$. Planned comparisons showed that both the validity benefit (i.e., the difference between valid and neutral trials), $t(19) = 2.32$, $p = .032$, and the invalidity cost (i.e. the difference between invalid and neutral trials), $t(19) = 2.64$, $p = .023$, were larger for the 80% valid condition compared to the 50% valid condition. Both the validity benefit and invalidity cost were present (i.e. significantly different than zero) for both reliability conditions (ts>2.37, ps<.028).

Precision

The average precision in each condition is shown in Figure 2B. Again there was a main effect of validity on precision, *F*(2, 38) = 74.54, *p*<.001, η_p^2= .80, none of reliability, *F*(1, 19) = .04, *p* =.838, η_p^2= .01, and a reliability x validity interaction, *F*(2, 38) = 16.84, *p*<.001, η_p^2= .47. Both the validity benefit , *t*(19) = 2.31, *p* =.032, and the invalidity cost, *t*(19) = 3.68, *p* =.002, were greater in the 80% than in the 50% condition. The invalidity cost was significant for 80% valid condition, *t*(19) = 4.67, *p*<.001, but not for 50% valid condition, *t*(19) = .56, *p* = .580. The validity benefit was greater than zero in both conditions, (*t*s> 5.35, *p*s<.001).

Recall probability for the target

The average recall probability in each condition is shown in Figure 2C. There were main effects of reliability on probability, *F*(1, 19) = 5.06, *p* =.036, η_p^2= .21, and of validity, *F*(2, 38) = 13.75, *p*<.001, η_p^2= .42, and a reliability x validity interaction, *F*(2, 38) = 5.91, *p* =.018, η_p^2= .24. Planned comparisons showed that the validity benefit did not differ between the 80% valid and the 50% valid conditions, *t*(19) = 1.41, *p* =.174, while the invalidity cost was larger for the 80% valid condition compared to the 50% valid condition, *t*(19) = 2.12, *p* =.047. The validity benefit was present (i.e. significantly different from zero) for both conditions (*t*s>2.16, *p*s<.044), while the invalidity cost was present in the 80% valid condition, *t*(19) = 2.45, *p* =.024, but not the 50% valid condition, *t*(19) = .26, *p* = .795.

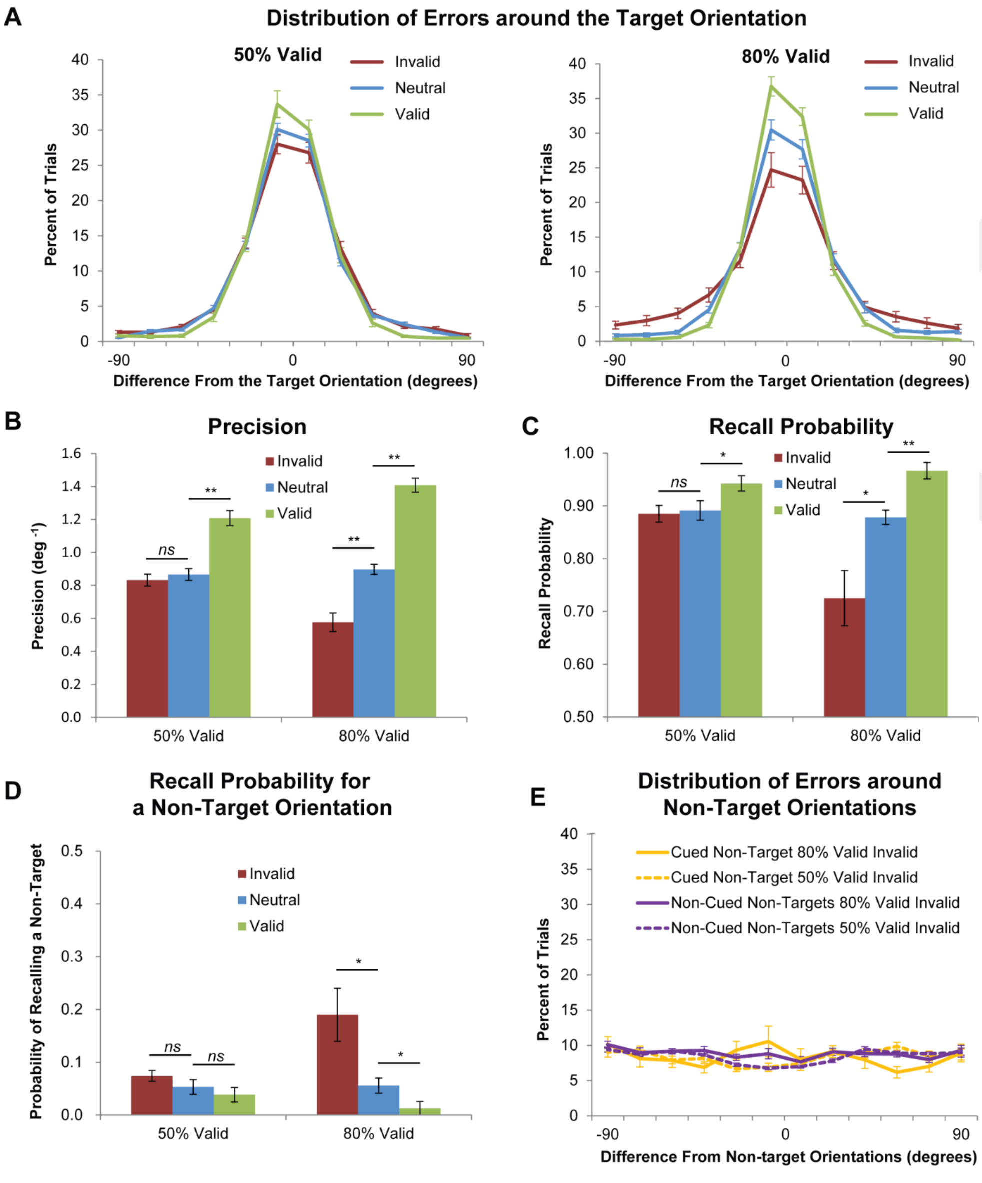

Figure 5.2. (A) Distribution of errors relative to the target (i.e. probed) orientation for 50% valid (left panel) and 80% valid (right panel) conditions. (B) Precision for the target, (C) recall probability estimate for the target, and (D) recall probability estimate for a non-target for each condition. The invalid, neutral and valid trials are shown in red, blue, and green respectively. (E) Distribution of errors on invalid trials relative to non-target orientations. The error bars represent standard mean errors for standardized data (i.e. corrected for between-subjects variance, Cousineau, 2005). The ns, '*' and '**' represent p>.05, p<.05 and p<.005 respectively.

Recall probability for non-targets

The average probability of recalling a non-probed item in each condition is shown in Figure 2D. There was a main effect of validity, $F(2, 38) = 7.09$, $p=.013$, $\eta_p^2= .27$, and none of reliability on this probability, $F(1, 19) = 1.61$, $p =.220$, $\eta_p^2= .08$. Again, there was a reliability x validity interaction, $F(2, 38) = 4.66$, $p =.039$, $\eta_p^2= .20$. Planned comparisons showed that the validity benefit (in terms of a lower likelihood of recalling a non-probed item on valid than on neutral trials) was not different for 80% valid and 50% valid conditions, $t(19) = .12$, $p =.904$, even though it was significant, in post-hoc tests, only in the 80% valid, $t(19) = 2.15$, $p =.045$, and not in the 50% valid condition, $t(19) = 1.08$, $p =.294$. The invalidity cost, meanwhile, was higher for 80% valid condition compared to 50% valid condition, $t(19) = 2.09$, $p =.051$. The probability of reporting a non-probed item was greater for invalid trials compared to neutral trials only in the 80% valid condition, $t(19) = 2.36$, $p =.029$, but not in the 50% valid condition, $t(19) = .99$, $p =.336$.

In order to test if the high probability of reporting a non-target item was driven by reporting the cued non-target or any of the (non-cued) non-targets, we compared the error distributions around the orientation of the cued non-target and non-cued non-targets (see Figure 2E). The distribution of responses around the cued non-target on 80% valid trials was somewhat steeper compared to the cued non-target on 50% valid trials and compared to non-cued non-targets in both reliability conditions (although the difference in percentage of errors at -7.5 and 7.5 degrees did not reach significance, ts < 1.73, ps > .100). This leaves open the possibility, although statistically not supported, that the higher non-target recall probability on 80% invalid trials in comparison to other conditions is due to recalling the cued non-target on a greater proportion of trials than recalling any other non-target.

Discussion

The findings support the idea that the degree of retro-cue effects on recall performance depends on the reliability of the cue. The cost of invalid cueing was minor for raw deviation, and altogether absent for precision and recall probability estimates when the cue was relatively unreliable (i.e. 50% valid), while there was still a clear benefit for valid cues. When the cue was more reliable (80% valid), benefits were larger, and now costs were also present. Furthermore, on invalid trials, the likelihood of mistakenly reporting a non-probed item during test was higher when the cue was more reliable. These results suggest that how participants implement the retro-cue to the memory task is, at least partly, under strategic control: When the cue has low reliability, observers prioritize the cued item for maintenance and/or retrieval without letting go of the non-cued items (Prioritization During Maintenance and Prioritization During Retrieval) probably in anticipation of the still quite likely event of being tested on one of the non-cued items. As a result invalid cueing costs are at most minor. In contrast, when the cue is highly reliable, in addition to prioritization, attentional and/or memory resources are disengaged from non-cued items during maintenance (Protection and Removal), which leads to a high invalidity cost when a non-cued item is probed. Retro-cue effects thus seem to be in line with the Prioritization During Maintenance or Prioritization During Retrieval hypotheses when cue validity is low, but in line with the Protection or the Removal hypotheses when cue validity is high.

Cue reliability may not be the only contributing factor in determining invalidity costs. For example, Astle et al. (2012) found that invalid cues had a cost on recognition accuracy only when memory set size exceeded the VWM capacity limit (i.e. eight), but not for set sizes within the VWM capacity limit (i.e. two and four, but see van Moorselaar, Olivers, Theeuwes, Lamme, & Sligte, under review-b), despite the fact that their cue was 80% valid. Using the same set size and the same cue reliability, in the present study we observed a cost of invalid cueing. Our study and that of Astle et al. (2012) differ in the test used to measure memory performance. We believe that the continuous report procedure used in the present study is a more sensitive memory measure and therefore might reveal differences in performance that are less likely to be detected with the discrete same/different judgment task that was used by Astle et al. (2012), because it provides a measure of how good the response is for each trial instead of reducing the response to a binary decision (Wilken & Ma, 2004). Consistent with this claim, in the present study, the effects of retro-cueing were more pronounced for precision compared to the recall probability of items. Nevertheless, we cannot exclude the possibility that invalidity costs might be smaller, although not completely absent, for smaller set sizes even with a continuous recall measure since the possibility of being tested on a particular non-cued item is higher, and also maintenance is less demanding for smaller set sizes. Both of these factors make it less beneficial to redistribute attentional/memory resources when the set size is small.

Notwithstanding the role of set size, our findings suggest that some of the inconsistency in results on invalidity costs is due to differences in the reliability of the retro-cue (for a similar argument for directed forgetting cues, see Williams & Woodman, 2012). Thus, the absence of an invalidity cost in Rerko and Oberauer (2013) may merely reflect a lack of attentional redistribution due to the low reliability of the retro-cue, rather than the absence of a role of attention in VWM maintenance. Our results suggest that attentional redistribution is performed mostly for highly reliable cues (as in 80% valid cue condition in the present study) and that without being attended, VWM representations are vulnerable to interference and/or decay – consistent with earlier claims (Astle et al., 2012; Makovski & Jiang, 2007; Makovski et al., 2008; Matsukura et al., 2007; Pertzov et al., 2013; van Moorselaar et al., under review-a). Another possibility is that non-cued items are actively removed from memory when cues are highly reliable, as this would also result in significant invalidity costs (Kuo et al., 2012; Souza et al., 2014; Williams & Woodman, 2012). Considering that previous research has provided support for both mechanisms, we believe that they may both occur. On some trials non-cued items may be actively removed from memory, whereas on other trials they are attended less, and therefore more vulnerable to interference. The important conclusion we want to make is that either mechanism is more likely to be implemented when the cue is highly reliable.

Regardless of these exact mechanisms, our findings point to a dissociation between how retro-cues affect the cued and the non-cued items. While one is attended, the other may be unattended but is not necessarily dropped (Rerko & Oberauer, 2013). Instead whether a non-cued item is maintained or not may be a separate decision. Such a dissociation is consistent with several models promoting a distinction between memory items that are in the current focus (“template”) and other VWM representations that are held prospectively, or “on reserve” (LaRocque et al., 2013; LaRocque et al., 2014; Oberauer, 2002; Olivers et al., 2011; Rerko & Oberauer, 2013; van Moorselaar et al., under review-b; van Moorselaar, Theeuwes, & Olivers, In Press; Zokaei et al., 2014a). These two types of VWM representation may have different mechanisms of maintenance, which operate more or less independently: 1. Task-relevant (here cued) representations are carried into a prioritized template status (which may also prioritize them for retrieval) regardless of the cue reliability, as there is little to lose by doing so. In line with this Berryhill, Richmond, Shay, and Olson (2012) demonstrated the presence of a validity benefit even when the cue was only informative on a minority of trials.. 2. Currently irrelevant non-cued items are held via a more passive accessory storage, and observers may decide to remove these depending on the perceived reliability of the cue - that is depending on whether they see a potential future use for them.

In short, present results show that how retro-cues affect recall performance depends on the reliability of the cues. When highly reliable, retro-cues resulted in major invalidity costs and larger validity benefits as compared to low reliable retro-cues that resulted in minor invalidity costs and smaller validity benefits),Thus, cue reliability will have to be considered before drawing any conclusions from research using probabilistic retro-cues.

Chapter 6

The loss of information from visual working memory depends on retro-cue reliability: Evidence from EEG

Gunseli, E., Fahrenfort, J., Daoultzis, K., Meeter, M., & Olivers, C. N. L. (in prep). The loss of information from visual working memory depends on retro-cue reliability: Evidence from EEG.

Abstract

Cueing attention to a representation in visual working memory (VWM) has been found to improve recall and recognition performance. However, the fate of unattended VWM representations is currently less clear, as some studies have reported costs for non-cued representations, while others have not. We recorded EEG while participants performed a VWM task. Retro-cues indicated which of several representations was most likely to be tested. We manipulated the retro-cue reliability between blocks (i.e. the ratio of valid to invalid cue trials). The allocation of attention to the cued representation was tracked through the N2pc after the retro-cue, and through decoding accuracy for the cued location in alpha band power (i.e. 10-14 Hz) during the maintenance interval. Both measures indicated that attention was directed to the cued item through the maintenance interval regardless of reliability, but more strongly so for highly reliable cues. The fate of the non-cued representations was tracked through the contralateral delay activity (CDA), an index of VWM maintenance. It revealed that non-cued representations were dropped only after a highly reliable cue. Reconciling previously conflicting results, the results show that the mechanisms of maintenance of VWM representations can be dissociated from attention within VWM.

Introduction

The human ability to successfully attend to and remember relevant information is essential for performing a variety of cognitive tasks, and is correlated with intelligence (Carpenter, Just, & Shell, 1990; Fukuda et al., 2010; Kane & Engle, 2002; Luck & Vogel, 2013; Newell, 1994). Although attention and working memory (WM) have been proposed as separate constructs, there is growing evidence that suggests they are intertwined (Engle, Kane, & Tuholski, 1999; Kane, Bleckley, Conway, & Engle, 2001), and might even reflect the same neural mechanisms (Kiyonaga & Egner, 2013; Postle, 2006; Theeuwes, Belopolsky, & Olivers, 2009). For example, spatial WM maintenance has been shown to involve attending to maintained locations (Awh et al., 1998). Similarly, focusing attention on a single representation within visual WM (VWM) has been found to improve maintenance of this representation, relative to conditions where none of the representations were selectively attended (for reviews, see Awh & Jonides, 2001; Gazzaley & Nobre, 2012). However, research has provided conflicting results whether attending to one item has consequences for the other, unattended items within VWM, leading to opposing views on the role of attention in VWM maintenance. The present study was performed to help resolving this controversy. We tested whether VWM is essentially internally oriented attention, or VWM and attention are distinct mechanisms.

The role of attention in VWM has typically been studied using retrospective cues (“retro-cues”), although other manipulations such as recency have also been used (Zokaei et al., 2014b). A retro-cue is a signal that indicates which of the several memory representations is likely to be the relevant one for the task at hand. Importantly, a retro-cue is shown after the presentation of the memory items; it therefore acts retrospectively. As can be seen in Figure 1, most commonly they are visual-spatial cues pointing the location of the memory item as it was presented in the memory display. Retro-cues have been suggested to result in the internal attentional selection of the cued representation within VWM in a similar way as attentional selection operates on objects in the external world, and relying on similar brain regions (Nobre et al., 2004). The consequence is better memory performance for the attended representation compared to the unattended representations (Griffin & Nobre, 2003; Lepsien et al., 2005; Sligte et al., 2008).

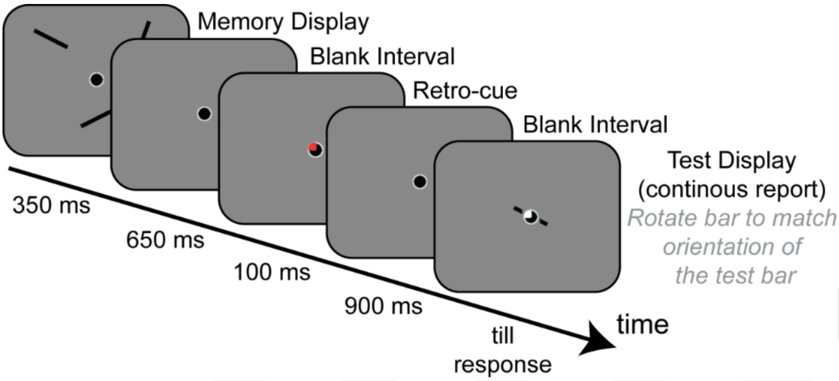

Figure 6.1. The retro-cue experimental procedure. Participants were asked to remember the three orientations shown in the memory display. After a blank interval a retro-cue was presented pointing to the location of the item (in this example top-left) that was most likely to be tested. Retro-cues were not always valid. Following a second blank interval the test display was presented during which participants were asked to rotate a randomly-oriented bar to match the orientation of the probe item (which in this example is the one presented on top-left, hence making the retro-cue valid).

Although converging evidence suggests that attending to a representation within VWM improves its recall performance, the fate of the *unattended* representations is less clear. In order to study memory performance for unattended representations, on some proportion of trials a non-cued representation is probed at test. A lower memory performance on these *invalid* cue trials compared to *neutral* or no-cue trials is referred to as an invalid cueing cost. An invalid cueing cost implies that VWM representations are impaired when attention is allocated away from them. However, results have been conflicting, Some studies have observed costs of invalid cueing whereas others have not, leading to opposite conclusions regarding the role of attention on VWM maintenance. On the one hand, studies that failed to observe invalid cueing costs have suggested that allocating attention away from VWM representations does not impair memory, hence attention is not necessary for successful VWM maintenance (Landman et al., 2003; Rerko & Oberauer, 2013). This explanation is consistent with the recent neuro-evidence that shows one representation in VWM can be prioritized without any costs for non-prioritized representations (LaRocque et al., 2014; Lewis-Peacock et al., 2012; Lewis-Peacock & Postle, 2012; Zokaei et al., 2014a). On the other hand, the studies that observed invalid cueing costs claimed that attention is necessary for successful VWM maintenance (Matsukura et al., 2007; Pertzov et al., 2013), which is in line with studies that suggested focusing attention on a representation within VWM protects it from interference by other representations and new visual input (Makovski et al., 2008; Pertzov et al., 2013; van Moorselaar et al., 2015). Therefore, reaching a consensus regarding the costs of invalid retro-cueing has important implications for understanding the role of attention in VWM maintenance.

Recently, we (Gunseli et al., 2015) proposed that these inconsistent findings might be due to the differences across studies in the retro-cue reliability (i.e. the proportion of valid to invalid retro-cue trials). Typically, the studies that failed to observe invalid cueing costs used lower retro-cue reliabilities (Landman et al., 2003; Lepsien & Nobre, 2007; Rerko & Oberauer, 2013) than studies that observed invalid cueing costs (Astle et al., 2012; Matsukura et al., 2007; Pertzov et al., 2013).[5] Reconciling these contradictory findings, Gunseli et al. (2015) found invalid cueing costs only when the retro-cue had a high reliability (i.e., 80% valid), but not when it had a lower reliability (i.e., 50% valid). On the other hand, benefits of valid retro-cues were observed in both conditions, though they were larger for 80% valid cues. These results suggest that when the retro-cue has a high reliability, attention is strongly allocated to the cued representation - making the non-cued representations more likely to be forgotten - whereas when the retro-cue has a low reliability participants attend to the cued representation while also maintaining the non-cued representations in VWM. The latter implies that attending to one VWM representation does not necessarily entail forgetting others. In other words, although attention improves memory performance, it might not be necessary for maintenance per se.

However, although Gunseli et al. (2015) showed that the inconsistent results in the literature regarding the invalid cueing costs can be explained by the differences in the reliability of retro-cues, there are two questions that cannot be answered using behavioral data. The first question is whether, for highly reliable retro-cues, invalid cueing costs are due to non-cued representations being dropped during the maintenance interval, or them being unattended and therefore becoming more vulnerable to interference from the test display. Under the first view, costs arise early, after the cue, whereas under the second view, they arise at test. There is electroencephalogram (EEG) evidence that supports the claim that non-cued representations are dropped from VWM following a 100% valid retro-cue (Eimer & Kiss, 2010; Kuo et al., 2012; for a similar effect using forgetting cues, see Williams & Woodman, 2012). The second view, which suggests unattended VWM representations become more vulnerable to interference at test, is consistent with the claims that attention protects VWM representations from interference by new visual input (Makovski & Pertzov, 2015; Makovski et al., 2008; van Moorselaar et al., 2015). Hence, the question remains unanswered with evidence supporting both views.

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[5] Although the studies that failed to find an invalid cueing cost also typically had a second retro-cue counteracting the first one, we believe this factor itself cannot account for the absence of invalid cueing costs since Matsukura et al. (2007) observed an invalid cueing costs in a double-cueing paradigm when the reliability of the first retro-cue was high.

The second question is whether, when the retro-cue has a low reliability, the cued representation is prioritized during *maintenance* (as proposed by the two views presented above), or merely at *retrieval,* without any attentional reallocation during maintenance. The claim that the cued representation is prioritized at retrieval was made by studies that failed to observe invalid cueing cost on recognition accuracy but found costs on RT (Astle et al., 2012; also see Nobre et al., 2007, for electrophysiological evidence of prioritization during retrieval). This claim is in line with resource models of memory and attention (Alvarez & Franconeri, 2007; Bays et al., 2009; Bays & Husain, 2008; for a review, see Franconeri, Alvarez, & Cavanagh, 2013), which would predict that the benefits for cued representations should inevitably be accompanied by costs for non-cued representations, since the benefits would be due to the reallocation of attentional resources from the non-cued to the cued representation. The results from the low reliable cue condition of Gunseli et al. (2015) showed retro-cue benefits in the absence of costs. Therefore, it might be that the cued representation is only prioritized at retrieval when the retro-cue has a low reliability, without any attentional reallocation during maintenance.

In order to test these possibilities, the present study used EEG recordings that enabled investigating the allocation of attention and maintenance in VWM via their electrophysiological indices. We used both event-related potentials (ERPs) and pattern classification in the time-frequency domain to track a) the attentional selection of the cued representation, b) the maintenance of representations within VWM, and c) the allocation of attention during VWM maintenance. Within the ERP signal, we looked at the posterior contralateral N2 (N2pc), and the Contralateral Delay Activity (CDA). The N2pc is a negativity over the parietal electrodes on the hemisphere contralateral to attended stimuli, and has been suggested to reflect the attentional selection of an item over others, both for internal representations and objects in the external world (Dell'Acqua et al., 2010; Eimer, 1996; Hickey et al., 2009; for a review, see Luck, 2012; Luck & Hillyard, 1994b). Thus, we used the N2pc to measure the strength of the attentional selection of the cued representation within VWM. The CDA is a sustained negativity over the parietal-occipital electrodes on the hemisphere contralateral to remembered stimuli. It has been observed to be sensitive to the VWM load, and been claimed to be an index of VWM maintenance (Ikkai et al., 2010; Klaver et al., 1999; Vogel & Machizawa, 2004). Accordingly, we used the CDA to track the maintenance of representations in VWM. In particular, we reasoned that if non-cued representations are forgotten following a retro-cue, then a CDA should emerge after the retro-cue, since now there would be an imbalance in the number of items maintained in each hemisphere (as an item would be maintained on the cued side, but not on the non-cued one). On the other hand, if non-cued representations are kept in VWM, there would be no imbalance occur and no CDA would emerge after the retro-cue.

Within the frequency domain, we looked at alpha band activity (8-14Hz) recorded over parietal and occipital electrodes, which has been associated with the active inhibition that is used for attending to relevant over irrelevant information in a sustained fashion. Again, this has been suggested to be true whether attention is allocated externally in the world or internally in memory (for a review, see Klimesch, 2012; Van Der Werf et al., 2008; van Dijk et al., 2010; Worden et al., 2000). In line with this, successful classification on the alpha band for a cued location has been suggested to track the allocation of visual-spatial attention to that location (Myers et al., 2014; Treder et al., 2011). Hence, we used the accuracy of decoding the location of the retro-cued representation on the alpha-band as an index of sustained allocation of attention during VWM maintenance.

The experimental procedure is shown in Figure 1. We used a continuous report memory recall task to obtain a sensitive measure of memory performance (Bays & Husain, 2008; Zhang & Luck, 2008). The memory display contained three lines of orientations, one on the vertical midline and two bilaterally at an equal distance to the center. The two lateral locations allowed us to measure an N2pc and CDA to a retro-cued item, since both components require a lateral asymmetry in the location of the attended and maintained item respectively. After a blank interval, a retro-cue indicated which of the memory representations was most likely to be tested by retrospectively pointing its location in the memory display. The retro-cue was not always valid, as on so-called *invalid* trials the cued representation was not going to be tested. Critically, following Gunseli et al. (2015), the retro-cue reliability (i.e. the proportion of valid to invalid trials) was manipulated across blocks being either 50% valid or 80% valid.

Based on the results of Gunseli et al. (2015), we expected larger behavioral effects (i.e. difference between invalid and valid trials) in 80% valid condition compared to the 50% valid condition. Moreover, we hypothesized that, if valid cueing benefits reflect stronger attentional selection of the cued item, we would observe an N2pc to the retro-cue, and above chance decoding accuracy on the alpha band for the location of the retro-cued representation in both reliability conditions, though larger in 80% valid condition. Whereas if cueing benefit is merely due to prioritization during retrieval, which can be expected for the 50% valid condition, then there would be no N2pc nor above chance decoding accuracy in this condition. Crucially, if invalid cueing costs indeed reflect non-cued representation being dropped from VWM, we would observe a CDA only in the 80% valid blocks in which there were invalid cueing costs. This dissociation between effects of retro-cue reliability on the N2pc and decoding accuracy on the one hand, and on the CDA on the other, would suggest that attending to a VWM representation does not necessarily entail forgetting others.

Method

Thirty-two healthy volunteers participated in the experiment for course credit or monetary compensation. Two participants were excluded; one due to excessive noise in their EEG recordings and one due to poor behavioral performance (see Data Analyses), leaving 30 participants of whom the data was analyzed. The study was conducted in accordance with the Declaration of Helsinki and was approved by the faculty's Ethical Committee. Written informed consent was obtained.

The procedure is shown in Figure 1. Each trial started with the presentation of the fixation circle of radius .33º, for a duration jittered between 1200-1600 ms. Then, the memory display was presented for 350 ms. It consisted of three black oriented bars (2.08º x 0.25º visual angle) located at 60 (right), 180 (bottom) and 300 (left) degrees relative to the top of an imaginary circle of radius 3.50º. The orientation of each bar was chosen at random with the restriction that bars within the same trial differed by at least 10º. The retro-cue was presented for 100ms following a blank interval of 650 ms during which the fixation circle was presented.. The retro-cue was the same as the fixation circle except that a quarter (90º) of it was filled with either red, 27.08 Cd/m^2, or green, 24.10 Cd/m^2, depending on the reliability condition (order counterbalanced). For the initial practice phase where the cue was 100% valid, the retro-cue fill color was orange (53.46 Cd/m^2). Following the retro-cue, there was a blank interval of 900 ms in which the fixation circle was presented. Then the test display was presented till response. It contained a probe cue pointing to the location of the probed representation and a randomly oriented probe bar that were both presented at the center of the screen. This probe cue was the same as the retro-cue except that the fill of the quarter was white. Participants were asked to indicate the precise orientation of the bar at the probed location by rotating the probe bar using the mouse, and pressing the left mouse button. After a mouse response was made, the correct orientation was indicated by a central white bar for 100 ms. The screen was empty during the inter-trial interval which was jittered between 1200-1600 ms.

The retro-cue was either 80% or 50% valid within a 250-trial block (500 experimental trials in total). Each validity condition (i.e. valid and invalid) was randomly intermixed within the block. Before each reliability condition, participants were informed about the validity ratio of the cues (as was also indicated by the color of the cue), and they performed a practice session of 25 trials to get used to this particular validity ratio. Moreover, at the beginning of the experiment, there was an initial practice session of 25 trials with a 100% valid cue to make participants familiar with the cue. At the end of each block, participants received feedback on block average and grand average memory deviation values.

Data Analysis

Behavior

Deviation scores on the memory test were calculated as the average difference (i.e. error) between the original orientation of the probed memory bar and the orientation of the response. One participant with an average deviation lower than 2.5 standard deviation below the grand average of the group was excluded from analysis. The precision was calculated, per condition, as the inverse of the standard deviation of the error in subjects' responses (Bays et al., 2009). The deviation scores were entered into a model to calculate the probability of recall for the target and non-target VWM representations (Bays et al., 2009). For each condition, raw deviation, and probability of recall and precision estimates for the target were entered into a repeated-measures

EEG Recording

The electroencephalogram (EEG) and electro-oculogram (EOG) were recorded from 70 sintered –AG/AgCl electrodes positioned at 64 standard International 10/20 System sites and 6 external locations mentioned below, using the Biosemi ActiveTwo system (Biosemi, Amsterdam, the Netherlands). No impedance measurements or gain adjustments are needed with the ActiveTwo system (www.biosemi.com). The vertical EOG (VEOG) was recorded from electrodes located 2 cm above and below the right eye, and the horizontal EOG (HEOG) was recorded from electrodes 1 cm lateral to the external canthi. The VEOG was used in the detection of blink artifacts, and the HEOG was used in the detection of horizontal eye movement artifacts. Electrophysiological signals were digitized at 512 Hz.

ERP analysis: N2pc and CDA

All ERP analyses were carried out using the EEGLAB toolbox (Delorme & Makeig, 2004), the ERPLAB toolbox (Lopez-Calderon & Luck, 2014), and custom scripts implemented in MATLAB (The MathWorks, Inc., Natick, MA). All ERPs were computed with respect to a 200 ms pre-stimulus baseline period, between -200 to 2000 ms around the memory display, and were re-referenced offline to the average of left and right mastoids. The data was filtered with an IIR Butterworth filter with a bandpass of .01 – 40 Hz. Trials with ocular artifacts or large voltage shifts were excluded. The artifact rejection was performed using our standard methods (see Gunseli et al., 2014b), using the artifact detection functions of the ERPLAB toolbox. The rejection of horizontal eye movements was performed in two steps. First, the single-trial waveforms were inspected to determine an optimum threshold for each participant that rejected a high proportion of the trials with artifacts, while keeping a relatively low proportion of artifact-free trials (Woodman & Luck, 2003). The second step involves the rejection of the individuals with a residual HEOG activity greater than 3.2 µV (i.e. residual eye movements greater than .2º, propagated voltage greater than .3 µV at posterior sites, see Lins et al., 1993a, 1993b). No dataset was rejected at the second step. Individuals were excluded from analyses if, after all the artifact rejections, the remaining number of trials per bin was lower than 80 trials. This led to the rejection of one participant. For the remaining participants, on average 9.8% of all trials were rejected by artifact detection functions mentioned above.

The N2pc and the CDA was calculated as the difference waves between electrode sites contralateral versus ipsilateral to the location of the retro-cued item. Based on previous studies, the N2pc to the retro-cue display was measured at P7/8, PO7/8, and O1/2 between 200 to 300 ms after the onset of the retro-cue, which corresponded to 1200 to 1300 ms after the onset of the memory display (for a review, see Luck, 2012). Based on previous studies, the CDA to the memory display was measured at P5/6, P7/8, PO7/8, and O1/2 between 300 to 900 ms after the onset of the memory display (McCollough et al., 2007), relative to the retro-cud location, as a neutral baseline since the location of the items were symmetrical around the midline. Similarly, for calculating the CDA resulting from the retro-cue, we took the interval 300 to 900 ms after the onset of the retro-cue (i.e. 1300 to 1900 ms after the onset of the memory display). The N2pc and CDA were entered into two ANOVAs with the within-subjects factors of electrode pair (mentioned above) and retro-cue reliability condition (50% valid; 80% valid). The CDAs following the memory display were compared against zero for both conditions using one-sample t-tests.

Time-frequency based decoding of the location of the retro-cued item

All decoding analyses were carried out using the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2010) and custom scripts implemented in MATLAB (The MathWorks, Inc., Natick, MA). Prior to the calculation of time-frequency representations (TFRs), the signal was epoched between -1000 to 2500 ms around the onset of the memory display. In addition to the same artifact detection methods used for ERP analyses, two new artifact detection functions were used to detect slow drifts and high-frequency noise in the data (which were already removed during the ERP analysis via filtering; pop_artstep and pop_artderiv, ERPLAB toolbox). The data was high-pass filtered at .1 Hz using an IIR Butterworth filter and then re-sampled to 64 Hz. Lastly, TFRs of total power, from 2 to 30 Hz in steps of 2, were calculated for each trial using a sliding time window of $\Delta T = 0.5$ s and multiplying the data in each time window with a Hanning taper.

Prior to decoding, in order to increase the signal-to-noise-ratio, TFR power values resulting from the time frequency analysis were binned using randomly selected triplets of trials from the same condition, without replacement, and each bin was averaged. To clarify, this was only done to increase the signal to noise ratio of the total power (evoked + induced), evoked power values or separate induced power values were not computed.

Subsequently, the data was split up into two parts, one for training and one for testing, using a 4-fold cross-validation scheme. Training and testing of the location of the retro-cued item was performed using a linear discriminant on the total power values, averaged per bin, from pre-defined parietal-occipital electrodes (P7, P8, PO7, PO8, P5, P6, O1, O2, Pz, POz, Oz, P1, P2, P3, P4, PO3, PO4) using the classify.m function of MATLAB. The training data was labeled by retro-cue location (left; right; bottom). The unlabeled test data were classified using the resulting classifier. The classification (i.e. decoding) accuracy was the ability of the classifier to successfully predict the retro-cue location. Above-chance (>33.3% accuracy) ability indicated that the multi-sensor patterns of activity contained information that discriminated between the location of the retro-cued items. Importantly, applying the classifier on TFRs instead of raw signal enabled testing which particular frequency band activity contributed to the discrimination ability.

The classification accuracy for each reliability condition (i.e. 50% valid and 80% valid) were tested against chance and also against each other at a group level using cluster-based permutation testing across both frequency and time dimensions (Maris & Oostenveld, 2007). A one-tailed t-test (80% valid > 50% valid) was performed on each decoding accuracy value per time-frequency. The samples (i.e. t-values for each time-frequency point) whose p-value was below .05 were selected. The selected samples were clustered based on spectral and temporal adjacency. Cluster level statistics were then calculated by taking the sum of the absolute t-values in each cluster separately for positive and negative t-values. These cluster level statistics were used in the nonparametric statistical test. For this test, 1500 permutations were performed at which the test statistics (i.e. sum of t-values per cluster) were calculated on randomly partitioned data (i.e. data whose condition labels 80% valid and 50% valid were randomly assigned to trials). The largest of the test statistics were selected for each random partition. Lastly, p-values for each cluster was calculated as the proportion of random partitions that resulted in a larger test statistic than the observed one. Additionally, the classification was performed for the lateral cues only to match the analyzed trials with the ERP analysis and the main statistical findings were similar to the classification analysis performed using all three retro-cue locations.

Results

Behavior

Raw Deviation

We looked at the effect of cue validity and reliability on raw deviations from the target orientation. Figure 2A shows the distribution of errors for each condition using bins of 15 degrees of deviations. The deviation was larger on invalid compared to valid cue trials,

$F(1, 29) = 27.75$, $p < .001$, $\eta_p^2 = .49$. Importantly, the difference between invalid and valid cue trials was larger when the cue was 80% valid compared to when it was 50% valid, as indicated by a validity x reliability interaction, $F(1, 29) = 6.49$, $p = .016$, $\eta_p^2 = .18$. There was no main effect of reliability on deviation, $F(1, 29) = 2.41$, $p = .131$, $\eta_p^2 = .07$.

Precision

The average precision in each condition is shown in Figure 2B. Again The precision was larger on valid compared to invalid cue trials, $F(1, 19) = 76.30$, $p < .001$, $\eta_p^2 = .72$, , and the difference between invalid and valid cue trials was larger when the cue was 80% valid compared to when it was 50% valid, as indicated by a validity x reliability interaction, $F(1, 29) = .02$, $p = .89$, $\eta_p^2 < .01$. Again there was no main effect of reliability, $F(1, 29) = 13.77$, $p = .001$, $\eta_p^2 = .32$.

Recall probability for the target

The average recall probability in each condition is shown in Figure 2C., Recall probability was larger on valid compared to invalid cue trials, $F(1, 29) = 18.98$, $p < .001$, $\eta_p^2 = .39$, and the difference between invalid and valid cue trials was marginally larger when the cue was 80% valid compared to when it was 50% valid, , as indicated by a validity x reliability interaction, $F(1, 29) = 3.41$, $p = .075$, $\eta_p^2 = .10$. There was again no main effect of reliability, $F(1, 29) = 2.71$, $p = .110$, $\eta_p^2 = .09$.

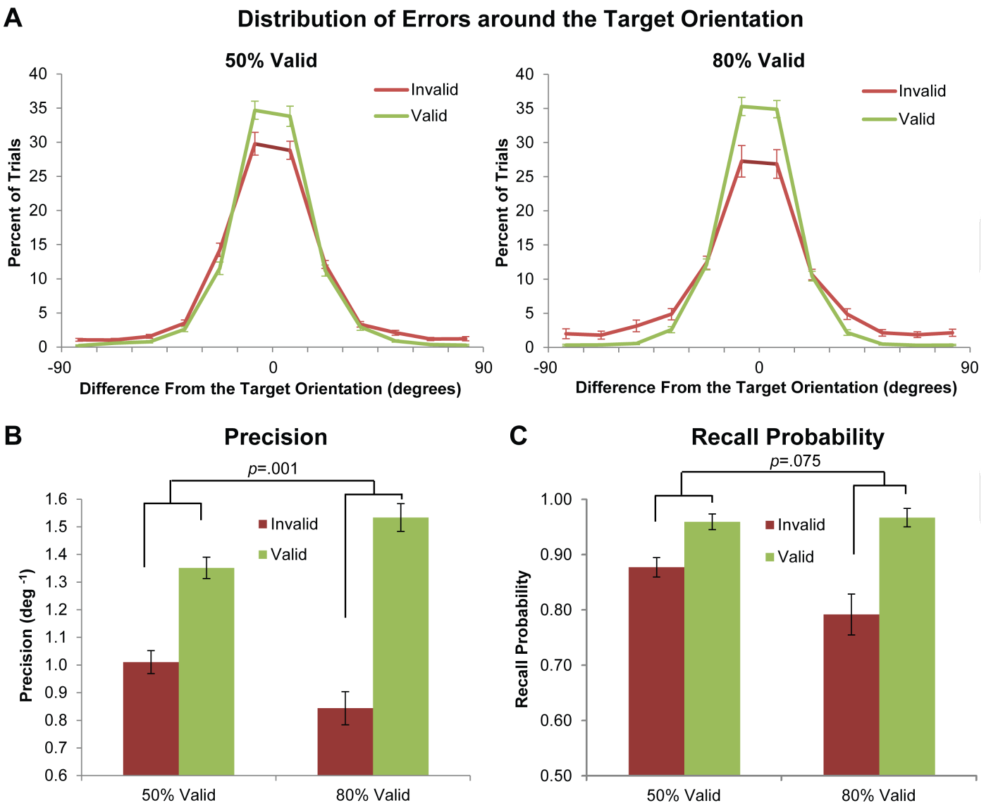

Figure 6.2. (A) Distribution of errors relative to the target (i.e. probed) orientation for the 50% valid (left panel) and 80% valid (right panel) conditions. (B) Precision and (C) recall probability estimates for the target in each condition. The invalid and valid trials are shown in different colors. The error bars represent standard errors of the mean for normalized data, i.e. corrected for between-subjects variance (Cousineau, 2005).

Electrophysiology

N2pc and the CDA

Figure 3A shows the contralateral and ipsilateral waveforms in respect to the location of the retro-cued item, averaged across the electrode pairs used in the analyses of the CDA (P5/6, P7/8, PO7/8 and O1/2).[6] We first analyzed the N2pc following the retro-cue. It was present for both the high reliable, $t(29) = 6.96$, $p < .001$, and low reliable cue conditions,

[6] The analysis of the N2pc excluded the P5/6 because the scalp topography of the N2pc has been suggested to be more ventral and lateral than the CDA (McCollough et al., 2007), though the statistical results were the same with or without the P5/6.

$t(29) = 5.34$, $p < .001$, though it was larger in the high reliable cue condition, $F(1, 29) = 12.02$, $p = .002$, $\eta_p^2 = .27$. There was no main effect of electrode pair, $F(2, 58) = 2.33$, $p = .106$, $\eta_p^2 = .07$, nor a cue reliability x electrode pair interaction, $F(2, 58) = .17$, $p = .839$, $\eta_p^2 = .01$.

The CDA was analyzed 300 ms to 900 ms after the memory display as a neutral baseline since the location of the items were symmetrical around the midline. As expected, there was no CDA following the memory display for neither of the conditions ($ts < .71$, $ps > .560$). Following the retro-cue, between 1300 to 1900 ms, the CDA emerged only in the high reliable cue condition, $t(29) = 2.21$, $p = .035$, but not in low reliable cue condition, $t(29) = .46$, $p = .645$. In line with this, the CDA was larger in the high reliable cue condition, $F(1, 29) = 7.39$, $p = .048$, $\eta_p^2 = .13$. There was no main effect of electrode pair, $F(2, 58) = .35$, $p = .787$, $\eta_p^2 = .01$, nor a cue reliability x electrode pair interaction, $F(2, 58) = .85$, $p = .472$, $\eta_p^2 = .03$.

Time-frequency based decoding accuracy

Figure 3B shows the accuracy of decoding the location of the retro-cued item across the time-frequency spectra separately for high reliable and low reliable cue conditions. Note that the chance level was 33.3% since there were three possible locations of retro-cued items. The decoding accuracy was above chance level for the clusters marked with a thin outline. The p-values of each cluster are shown next to it. Moreover, the decoding accuracy was larger in the 80% valid condition than in the 50% valid condition for three clusters marked with thick outlines as shown in the 80% valid panel, and numbered as (1) for the 2-4 Hz cluster between 1422 to 1562 ms., $p < .001$, (2) for the 10-14 Hz cluster between 1203 to 1375 ms, $p = .005$, and (3) for the 12-14 Hz cluster between 1484 to 1688 ms, $p < .001$.

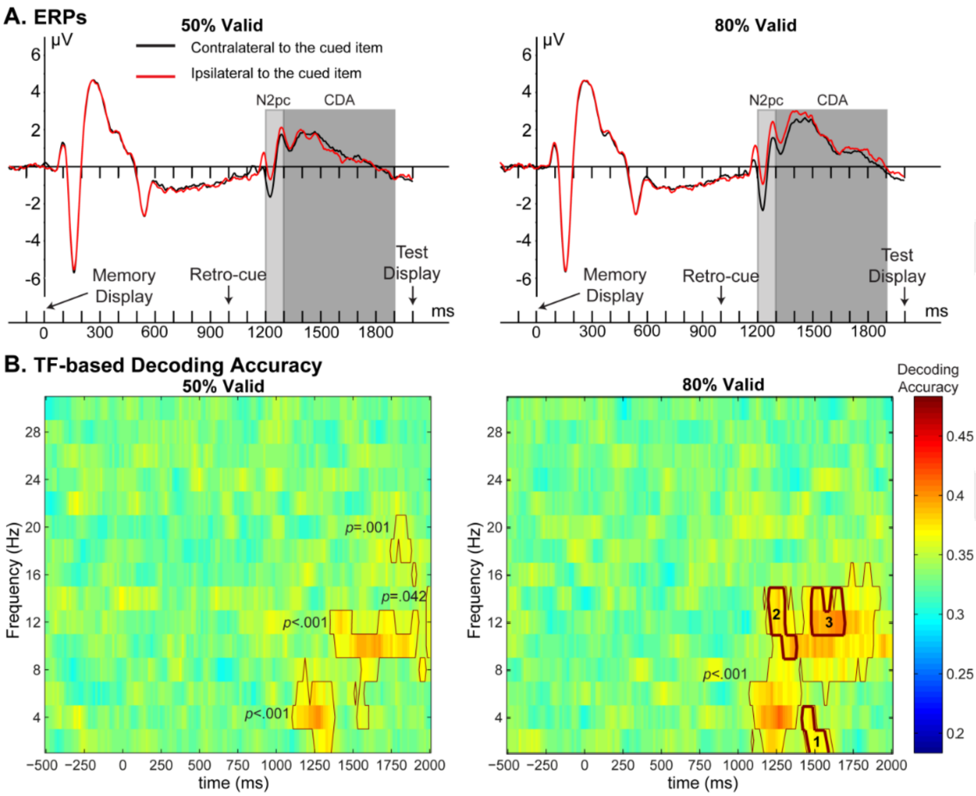

Figure 6.3. (A) The grand average waveforms at the average of PO7/8, P7/8, P5/6, and O1/2 electrode pairs, contralateral and ipsilateral to the location of the cue (in different colors) plotted separately for the 50% valid (left panel) and 80% valid (right panel) conditions. (B) The time-frequency-based decoding accuracy for the location of the retro-cued item, given separately for the 50% valid (left panel) and 80% valid (right panel) conditions. Thin outlines show the clusters at which the decoding accuracy was larger than chance level (i.e. 33.3%) and their p-values are provided next to each cluster. Thick outlines show three numbered clusters at which the decoding accuracy in the 80% valid condition was larger than in in 50% valid condition, (1) $p<.001$, (2) $p=.005$, (3) $p<.001$, calculated using non-parametric testing (Maris & Oostenveld, 2007).

Discussion

By using EEG indices of attentional selection (N2pc), attentional allocation during VWM maintenance (classification of attended location in the alpha band during maintenance), and VWM maintenance (CDA) the present study tested how retro-cues of different reliabilities change the way participants attend to and maintain cued and non-cued representations within VWM. The behavioral results showed that the recall performance was worse in invalid compared to valid retro-cue trials, and that this difference was larger for 80% valid compared to 50% valid retro-cues. The EEG results were in line with behavioral results. The N2pc to the retro-cue was observed in both reliability conditions, though it was larger following the 80% valid compared to 50% valid retro-cues. Moreover, the decoding accuracy for the location of the retro-cued item in the alpha band (8-14 Hz) was above chance level in both reliability condition, though it too was larger for 80% valid cues, during the retention interval following the retro-cue. Most importantly, a CDA was observed only following 80% valid retro-cues but not 50% valid retro-cues. These results are in line with our previous findings (Gunseli et al., 2015) and provide additional support for the claim that the degree to which participants use a retro-cue depends on its reliability. The present study extends this conclusion in several important ways:

1) The retro-cued representation is attended during *maintenance*, instead of being merely prioritized at *retrieval*, even when the retro-cue reliability is low. This argues against the idea that retro-cueing only affects retrieval.
2) Allocation of attention to the cued representation is stronger when the retro-cue reliability is higher, as indicated by higher N2pc amplitude and stronger classification of the cued position.
3) Non-cued representations are lost from VWM after retro-cues, at least on a subset of trials, but only if the cue has a high reliability. At low reliability, the absence of a CDA component suggested that all items were being maintained, despite attention being directed to the cued one.

Together, these results suggest that allocating attention to one VWM representation does not necessarily entail the loss of others. In other words, the process of attending to one item and the process of maintaining the others appear to be at least partially independent.

We found that when the retro-cue reliability is low, participants attend to the retro-cued representation while also keeping non-cued representations within VWM. Whereas when the retro-cue reliability is high, they attend more strongly to the cued representation and also drop non-cued representations from VWM. Thus, these results clarify why studies that typically used highly reliable cues observed invalid cueing costs while those that had lower retro-cue reliabilities did not. Our results also explain why a valid retro-cue is associated with stronger benefits when it is highly reliable. Unattended VWM representations have been claimed to be more vulnerable to interference from new visual input, such as the onset of the test display (Makovski & Pertzov, 2015; Makovski et al., 2008; van Moorselaar et al., 2015). Consequently, when cued representations are attended more strongly, such as when retro-cue reliability is high, they benefit from a stronger reduction in perceptual interference from the test display. Such interference may also explain why unattended representations in 50% valid condition had a lower recall probability estimate than attended ones even though the CDA suggested that they had been maintained in VWM during the retention interval. We suggest that, in the 50% valid condition, unattended representations were maintained through the blank interval but then suffered from interference by the test display to a greater extent than attended representations.

We observed that the loss of representations from VWM depends on the retro-cue reliability. This in turn suggests that whether to remove a representation from VWM might be a strategic decision that is based on the predicted future relevance of that particular representation. Such flexible control over VWM representations is consistent with the claims that attentional/memory resources can be flexibly distributed over representations (Bays & Husain, 2008; Franconeri et al., 2013; Zokaei et al., 2014b). However, we cannot exclude the possibility that the loss of VWM representations exclusively for highly reliable cues was due to an implicit priming effect instead being strategically driven. More specifically, participants might have implicitly learned to use the retro-cue to a greater extent when it is highly reliable as they experienced this to lead to success more often than in the case of low reliable retro-cues. Whether strategically driven or implicitly learned, our results show that the loss of representations from VWM depends on the task demands that indicate the future relevance of the particular representation

Our results are also in line with the studies that claim there are different states within VWM. Maximally one VWM representation has been argued to be in the focus of attention, with others outside this focus but nevertheless successfully maintained within VWM (LaRocque et al., 2014; Lewis-Peacock et al., 2012; Lewis-Peacock & Postle, 2012; McElree, 1998; Oberauer, 2002; Zokaei et al., 2014a). Evidence for this model comes from studies that observed elevated activation patterns for the retro-cued representation, and also showed that a previously non-cued representation can be carried back to the focus of attention and can be recalled successfully. Our results provides direct support for the claim that a representation can be at the focus of attention within VWM without losing non-focused representations by showing, within the same dataset, the concurrence of the electrophysiological indices of allocation of attention to the cued representation and maintenance of non-cued representation within VWM. This result argues against the claim that VWM merely reflects a distribution of internally oriented attention (cf. Kiyonaga & Egner, 2013; Postle, 2006; Theeuwes et al., 2009) and suggests that the mechanisms of maintenance of VWM representations can be partly dissociated from attention within VWM.

To our knowledge, our study is one of the first to show that a CDA can be used to track a change online in maintenance in VWM (causing an asymmetry in the spatial distribution of the remaining VWM representations). Previously, Kuo et al. (2012) observed a reduction in the amplitude of the CDA towards a lateralized set of items following a retro-cue (Duarte et al., 2013). But they observed a similar reduction in the neutral cue condition, which makes it difficult to conclude that the modulation was due to dropping representations from VWM. More in line with our present findings, Williams and Woodman (2012) observed a CDA emerging after retrospective cues asking people to forget the items on one side of the display. However, cues were presented only 350 ms after the onset of the memory display, and thus it is unclear whether it caused the dropping of already maintained items, or it prevented final encoding processes (e.g. from iconic memory, Di Lollo, 1977; Sperling, 1960). Lastly, Eimer and Kiss (2010) asked observers to remember a bilateral display. They were then asked to mentally search for a target in one side of the display, as indicated by a retro-cue. Eimer and Kiss (2010) found a negative contralateral deflection at posterior sites in response to the cue, which they linked to the CDA. However, this component did not last very long, and did not show the sustained hallmark of a typical CDA. Instead it might reflect the averaged and thus smeared out attentional orienting component towards the target in the search display, rather than maintenance (Dell'Acqua et al., 2010). Our results show more clearly that the CDA can be used to track the dropping of items from VWM.

In short, the present study shows that the loss of information from VWM depends on the retro-cue reliability. When the retro-cue reliability is low, the cued representation is attended while non-cued representations remain maintained within VWM. When the retro-cue reliability is high, the cued representation is attended to a greater extent than in low retro-cue reliability conditions. Moreover, non-cued representations are dropped from VWM on at least a portion of trials. Together, these results suggest that allocating attention to a representation within VWM has benefits for the attended representation, but that it does not necessarily entail the loss of unattended representations. In other words, the mechanisms of VWM maintenance are distinct from those of attending within VWM.

Chapter 7

Summary and Discussion

VWM and attention are known to interact with each other (Chun & Turk-Browne, 2007; Engle et al., 1999; Kane et al., 2001; Olivers, 2008). For example VWM representations that are maintained internally can guide attention externally. This guidance can even be involuntary, as it has been observed in conditions where participants knew that the VWM representation can never be the search target (Olivers et al., 2006; Olivers, 2009; Soto et al., 2005). The interaction between VWM and attention also works at another level: Attention can be directed to representations within VWM (Gazzaley & Nobre, 2012). In this case, attention operates internally in a similar fashion as the attentional selection works on the external world (Nobre et al., 2004) and improves memory performance for the attended representation compared to unattended representations (Griffin & Nobre, 2003; Lepsien et al., 2005; Sligte et al., 2008). The interaction between memory and attention is crucial for human functioning since there is a constant information flow that needs to be attended and remembered. In this dissertation, my aim was to contribute to the understanding of this interaction. Specifically, I investigated the effects of learning and task demands on 1) guidance of attention *by* memory representations, and 2) attention *to* memory representations.

Part 1. The Role of Memory Representations in the guidance of Visual Attention

Although the literature prior to this project provided plenty of evidence for interactions between WM and attention, many questions remained. One of those questions was why VWM, although it has been claimed to be central to attentional guidance, is neither sufficient nor necessary for attentional guidance. Specifically, most theories of attention claim that attentional guidance relies on attentional templates maintained in VWM. However, some studies have found that a VWM does not always guide attention, and EEG evidence suggests that attentional selection is possible in the absence of VWM templates. In **Chapters 2**, **3**, and **4**, I have shown that these paradoxical findings can be reconciled by taking into account two factors: 1) repeated search using the same attentional template results in its transfer from VWM to long-term memory (Carlisle et al., 2011), and 2) there are different states within VWM and not all contribute equally to attentional selection in the external world (for a review, see Olivers et al., 2011).

In the thesis, I have provided additional evidence for the claim that an attentional template hands off from VWM after repeated its repeated search, as indicated by a reduction in the CDA and the LPC, which are the ERP indices of VWM maintenance. In **Chapter 2**, I additionally showed that, although greater effort is invested for its maintenance, as indexed by a larger LPC, an attentional template for a difficult search task hands off from VWM at the same rate as an easy search task. This study also showed that the CDA was not sensitive to the amount of effort invested in the maintenance of a VWM representation.

Furthermore, I have shown that if a VWM representation is not prioritized, then it is not likely to guide attention. I have also found that a VWM representation can be prioritized either because it is task-relevant, or because the task-relevant representation has been transferred to long-term memory, leaving VWM free for a task-irrelevant representation. In the latter case, the task-irrelevant representation involuntarily guides attention to matching distractors. If there is no distractor that matches the task-irrelevant VWM representation, then the attentional template effectively guides attention from long-term memory. Hence, these findings bridge inconsistencies in the literature on memory-driven attention.

Remaining questions: What is learned through repeated search?

I have shown that learning modulates the status of task-relevant and task-irrelevant representations within VWM and consequently affects whether they can guide attention on the external world. Moreover, I have found that the search performance improves with repeated search, consistent with the theories of learning (Anderson, 2000; Logan, 1988; Shiffrin & Schneider, 1977). However, the improvement in search performance that I have observed in my studies occurs at a much faster pace (in a few trials) than that observed in previous studies (in tens or hundreds of trials). Furthermore, although previous studies have found that search efficiency improves with learning, I have observed an improvement only in search times but not in its efficiency. Together these findings suggest that there might be two types of learning, one at a representation level that occurs within a few trials, and other at a task level that is accomplished after many trials. When the same target is repeated a few times, its representation transfers from VWM to long-term memory. Whereas, when the same task is repeated over a long duration, not only the task-relevant representations but also the task requirements and strategies are learned. Although there is evidence supporting both levels of learning, the investigation of these within the same study is necessary for developing a better understanding of their similarities and differences.

Although the decrease in the VWM involvement for maintaining an attentional template has been taken as evidence for a transfer of its representation to long-term memory, direct evidence for this claim has been insufficient. Woodman and his colleagues have recently observed a decrease in the amplitude of P170, an ERP component that they have claimed to reflect the transfer to long-term memory, as a function of target repetition (Reinhart & Woodman, 2013; Woodman et al., 2013). However, in **Chapter 2**, I failed to replicate their findings. As mentioned there, consistent with earlier studies on P170 (or frontal selection positivity; Baas et al., 2002; Kenemans et al., 1993; Potts, 2004;

Potts & Tucker, 2001) we claimed that a decrease in P170 may reflect getting more efficient in the selection of the task relevant feature, which is the gap direction of the Landolt C. Therefore, a decrease in the P170 might be a *consequence* of long-term memory transfer, instead of reflecting the transfer itself per se. Thus, there is no consensus on a direct evidence for transfer of an attentional template to long-term memory. One of the reasons why obtaining a direct electrophysiological evidence for long-term memory transfer might be that long-term memory has been claimed not to rely on sustained neural activity but instead on synaptic changes (Bliss & Gardner-Medwin, 1973; Bliss & Lømo, 1973; Hebb, 2005). Therefore, a transfer to long-term memory might be a 'silent' process that is difficult to observe by EEG or other non-invasive neuro imaging methods.

Lastly, another remaining question is how long-term memory guides attention. One candidate is the facilitation of the perceptual efficiency of the target and/or the selection of the task response as a result of priming of the same target (Meeter & Olivers, 2006; Olivers & Meeter, 2006). However, the exact mechanisms of attention being guided by long-term memory remain unanswered. In order to investigate this, future studies need to look at the deployment of attention during visual search using direct measures of attention via eye tracking or EEG. For example, in order to test whether long-term memory templates result in a faster detection of the target, eye tracking data can be used to investigate the timing of the eyes fixating on the target. This would allow one to differentiate whether the benefit of long-term memory guidance is due to perceptual efficiency or to response selection, because only the former but not the latter predicts a faster selection of the target with its repeated search.

Part 2. The Role of Selective Attention in the Maintenance of VWM Representations

Another question related to the interaction between memory and attention has been regarding the fate of unattended representations within VWM. Although research has provided converging evidence that an attended representation is protected from interference by other representations (Pertzov et al., 2013) and by new visual input (Makovski et al., 2008; van Moorselaar et al., 2015), whether unattended representations are forgotten has been a debate. I have shown in **Chapters 5** and **6** that the fate of unattended VWM representations depends on the reliability of the retro-cues that indicate which of the VWM representations is likely to be task relevant. If a retro-cue has a low reliability, then participants keep maintaining non-cued representations. Nevertheless, the cued representation is attended and its recall performance improves. On the other hand, if a retro-cue has a high reliability, non-cued representations are forgotten, at least on some of the trials. Moreover, the cued representation is attended more when the cue is more reliable, and the memory performance improves to a greater extent compared to low reliable cues. These results contribute to the theories of WM and attention by showing that a VWM representation can continue to be maintained even when attention is directed to another representation within VWM. More specifically our results show that the mechanisms of VWM maintenance are distinct from those of attending to representations within VWM. So here too our findings have managed to bridge a theoretical divide in the literature.

Remaining questions: Are internal attention and prioritization the same?

I mentioned above that there are different states within VWM and that the task-relevant item has a prioritized status. I also described how attention can be focused to a particular VWM representation. The definitions of a prioritized status and an internally attended VWM representation are quite similar. Moreover, both can be obtained by retro-cueing the representation of interest. This raises the question whether a representation that is attended within VWM is the same as a representation that has a prioritized status: Essentially, whether these are just two different names for the same cognitive process. To date, there is no definitive answer. It might be that prioritization and attentional selection within VWM are distinct but overlapping processes. More specifically, an item that is attended might be gaining the prioritized status.

However, in order to answer these types of question, the nature of internal attentional selection and VWM must be understood well. For example, if attentional resources can be distributed flexibly across representations instead of being focused on only one representation at a time, a representation might be prioritized when the amount of attentional resources allocated to the representation reaches a particular threshold. This would imply that allocation of attention to a representation does not necessarily result in its prioritization within VMW, but only if it reaches a particular threshold. Alternatively, if attention can only be focused on one representation at a time, then any representation that is attended can be said to be also prioritized. Therefore, in order to answer whether attention and prioritization are the same mechanisms, first we need to develop a better understanding of how attention is distributed among VWM representations. I believe the recent improvements in brain imaging techniques and data analysis methods will help us developing this better understanding.

In particular, I have shown that the CDA is not sensitive to the effort invested for the maintenance of a VWM representation. Moreover, I have found that the CDA can be distinguished from classification in the alpha band, which has been suggested to reflect the internal attentional allocation within VWM representations. These findings suggest that the CDA is not a suitable tool to study the attentional dynamics within VWM. On the other hand, I have observed that the LPC is sensitive to the amount of effort invested in the maintenance of a VWM representation. Therefore, the LPC might be reflecting the *resource allocation* within VWM, whereas the CDA merely reflects *maintenance* in VWM.

Conclusion

To conclude, the chapters of this thesis shed new light on a) how memory representations guide attention in the external world, and b) how allocation of attention internally to VWM representations affect attended and unattended representations.

In the thesis, I have shown that only a prioritized VWM representation, or a so-called attentional template, guides visual attention. Moreover, repeated search for the same target results in the handoff of the attentional template from VWM, thus changing the status of task-irrelevant representations within VWM. This consequently affects whether task-irrelevant representations can guide attention on the external world. Therefore, automatizing search via learning comes at the expense of greater distraction because it leaves VWM free for prioritizing task-irrelevant information.

Attending to a representation within VWM, as directed by retro-cues, has been known to improve its recall performance. However, the fate of unattended VWM representations has been less clear. Reconciling previous contradictory findings, I have shown that the effects of retro-cues on cued and non-cued VWM representations are modulated by the reliability of these cues. If a retro-cue has a high reliability, participants focus on the cued representation and drop non-cued representations. Whereas, if a retro-cue has a low reliability, the cued representation is attended while non-cued representations are kept in VWM with none or minor loss of information. By showing that the allocation of attention to a VWM representation does not entail the loss of others, I have provided direct evidence for the claim that internal attention and VWM maintenance are not the same, though they are intertwined.

In sum, the chapters of this thesis support the interactive relationship between attention and VWM and clarify some aspects of this interaction by providing explanations for the conflicting findings and by eliminating alternative explanations of the existing results in the literature.

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Author Publications

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