博士論文

Storage systems in visuo-spatial working memory:
capacity independence and the role of attention

（視空間ワーキングメモリにおける保持システム：容量の独立性と注意の役割）

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Storage systems in visuo-spatial working memory: capacity independence and the role of attention

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General Introduction

How many items can we remember for a short period of time? Working memory (WM) is a mental function or functions underpinning such short time storage of memory. An important property of WM is its limited capacity, which means that there is a maximum number of items we are able to retain. Several studies have tried to estimate the maximum amount. Although, Miller (1956) first proposed that the maximum capacity as 7 ± 2 items, a following study by Cowan (2001) argued that it is more limited to approximately 4. Up to the present date, the latter view is widely accepted. In addition, this storage system does not seem to be limited to a unique source of information. The multi-component model of WM proposes that we have separated capacities of WM for visuo-spatial and auditory domains (Baddeley & Hitch, 1974).

The Multi-Component Model of Working Memory

The multi-component model of WM was proposed originally by Baddeley and Hitch (1974), and has been well accepted. They proposed that WM consists of three parts: the phonological loop, the visuo-spatial sketchpad and the central executive. The phonological loop and the visuo-spatial sketchpad are slave systems controlled by the central executive, dedicating themselves just to store information. The phonological loop retains auditory information, and the visuo-spatial sketchpad retains visual and spatial information. Each storage system has its own limited capacity. The central executive is an attentional system which manipulates the two slave functions.

The separation between the phonological loop and the visuo-spatial sketchpad has been supported by a large number of studies. For example, research using a dual task paradigm (i.e. a method combining two cognitive tasks to access their interference) showed that the performance of a visual memory task is disrupted by irrelevant visual inputs or a spatial tracking task, but not by irrelevant auditory inputs (e.g. an unattended speech). Similarly, a verbal memory task is not disrupted by visual or spatial tasks (Baddeley & Lieberman, 1980; Logie, 1986; Fougnies & Marois, 2011).

Further Functional Separations in the Visuo-Spatial Sketch Pad

Baddeley and Lieberman (1980) suggested that the visuo-spatial sketchpad is a unitary system. However, Logie (Logie, 1986; 1995; Logie & Marchetti, 1991) challenged this view and argued that the visuo-spatial sketchpad is comprised of separate components dedicated for visual and spatial information, respectively. In order to test this assumption, Logie and Marchetti (1991) inserted a secondary task (visual or spatial) during the retention interval of visual and spatial mnemonic tasks, and found that the visual task produced a larger interruption in the visual memory task than in the spatial memory task, and vice versa for the spatial task. These results indicate that the visuo-spatial sketchpad does not consist of a single system. Several studies utilizing dual task paradigm have replicated this visuo-spatial WM separation (Tresch, Sinnamon, & Seamon, 1993; Della Sala, Gray, Baddeley, Allamano, & Wilson. 1999; Klauer & Zhao 2004). Moreover, some neuropsychological cases have also supported this view (Farah, Hammond, Levine, & Calvanio. 1988; Hanley, Young, & Pearson.1991). For instance, a patient who had brain damage in tempro-occipital regions, the right temporal lobe, and the right inferior frontal lobe showed a disability in visual but not in spatial memory, whereas the opposite pattern was found in another patient who had damage in the right frontal area. These cases indicated that cortical regions underpinning visual and spatial WM are independent from each other.

Although many empirical findings in support of the visuo-spatial WM separation have been repeatedly reported and the theory seems to be now widely accepted, this theory is still not free from controversies (Luck, 2008). Moreover, the studies putatively supporting this view have a critical methodological issue. That is, almost all of the previous research has employed dual task paradigms, which combined a memory task and a concurrent non-memory task (e.g. a passive viewing of visual material during spatial memory task). Thus, strictly speaking, they have not reported direct evidence for the dissociation of two *memory* systems. To my knowledge, Wood (2011) was the first researcher that combined visual and spatial *memory* tasks and examined the visuo-spatial WM separation hypothesis more directly. In this study, it was shown that color and spatial WMs does not produce interference, thus supporting the hypothesized dissociation. However, he also found that shape and spatial WMs interfered with each other, indicating that two WM systems share the same storage resource. Since shape has been treated as a type of visual information, the result could undermine the visuo-spatial WM separation proposed by Logie (1995). Thus, more investigation is needed to clarify this issue.

The Role of Attention in WM Maintenance

Another line of argument that seems to be critical for the visuo-spatial separation hypothesis comes from the research on the relation between attention and visuo-spatial WM.

The recent literature on WM indicates that attention plays a crucial role for visuo-spatial WM processing (Awh, Vogel, & Oh, 2006). For example, Vogel, McCollough and Machizawa (2005) utilized an event related component (ERP) measurement and showed that selective attention works as a filter at the *encoding* stage of visual WM, which bounces unnecessary stimuli and let only the relevant items proceed into the WM storage. In addition, many studies have indicated that attention contributes to WM *maintenance* too (van Dijk, van der Werf, Mazaheri, Medendorp, & Jensen, 2010; Chun, 2011). If so, different types of attentional system might underpin different types of WM maintenance. It should be noted that attention can be dissociated into two different sub-systems; namely, visual and spatial attention (Scolari, Ester, & Serences, 2014). Spatial attention selects specific location and facilitates the processing of items presented in that location (Posner & Cohen, 1984). In contrast, visual attention (i.e. feature- and object-based attention) enhances processing of task-relevant features or objects regardless of their spatial location (Maunsell & Treue, 2006; Scolari et al., 2014). This distinction between attentional systems seems to correspond to the proposed visuo-spatial WM separation. Thus it has been argued that the same domain structure might underlies the organization of both attentional and WM sub-systems (Barnes, Nelson, & Reuter-Lorenz, 2001). Studies so far, however, have not reached a consensus on this issue.

On the one hand, many studies seem to support the correspondence between specific attentional and WM subdomains. First, Awh and his colleagues proposed the attention-based rehearsal theory of spatial WM, arguing that sustained spatial attention is the underlying mechanisms of spatial WM retention (Awh, Jonides, & Reuter-Lorenz, 1998; Awh & Jonides, 2001). Second, Luck and his colleagues argued that a visual WM contents including single visual features as well as multi-feature conjunctions are retained by an object-based system (Luck & Vogel, 1997; Vogel, Woodman & Luck, 2001), and spatial attention does not play any specific role for its maintenance (Zhang, Johnson, Woodman, & Luck, 2013). In addition, another line of evidence has also suggested that the role of spatial attention is limited to spatial WM maintenance (Woodman, Vogel, & Luck, 2001; Oh & Kim, 2004; Woodman & Luck, 2004) In the same vein, Barnes et al. (2001) suggested that object-based attention contributes to visual WM retention, but not to spatial WM.

On the other hand, some studies questioned that such correspondences truly exist. Wheeler and Treisman (2002) refuted the object-based retention theory of visual WM (Luck & Vogel, 1997; Vogel et al., 2001) and proposed that spatial attention is necessary for visual object WM. They argued that single features are stored in each separate storage systems, but the maintenance of integrated objects need spatial attention. Indeed, Wood (2011) found that object and spatial WMs interfered with each other, supporting this claim.

Furthermore, some recent studies have casted a doubt even on the role of spatial attention in spatial WM maintenance (Awh et al.,1998; Awh & Jonides, 2001). Belopolsky and Theeuwes (2009) and Chan, Hayward, and Theeuwes (2009) have reported counterevidence for this theory, and argued that spatial attention plays no functional role for spatial WM maintenance. Given that the attention-based rehearsal theory of spatial WM has been well accepted among researchers (Awh et al., 2006), these findings, if they are true, could undermine the foundation of the theory of domain specific correspondence between attention and WM. Therefore, further accumulation of evidence for this problem is needed.

The Current Dissertation

As I briefly reviewed so far, currently there is no comprehensive understanding about how the visuo-spatial WM sub-domains are separated, and how attention is related for their maintenance. The current dissertation focused on these two important issues, and provided evidence by carefully re-examining two critical previous findings. The first one was the shape-spatial WM interference observed by Wood (2011), and the second the controversy about the spatial attention rehearsal theory of spatial WM (Awh et al. 1998; Awh & Jonides, 2001).

Study 1 aimed to re-examine the shape-spatial WM interference observed by Wood (2011). For this aim, I used a dual task paradigm which combined a shape and spatial WM task. First, I tested whether some methodological confounds found in Wood's study (Wood, 2011) could account for the observed interference. Moreover, in case this possibility is discarded, I estimated the size of interference and evaluate its functional significance in relation to the visuo-spatial separation hypothesis.

Study 2 examined the attention-based rehearsal theory of spatial WM (Awh et al. 1998; Awh & Jonides, 2001), which assumes that spatial attention is continuously allocated to the remembered positions during the retention interval of spatial WM. To test this assumption, I utilized behavioral and ERP indices of spatial attention. In this regard, it should be noted that to show the effect of spatial attention is not a sufficient evidence for proving its functional significance in WM maintenance. For example, spatial attention could be observed even when it was produced as a mere after-effect of the WM encoding process. Thus, to test this possibility I inserted an attention-demanding visual search task during the spatial WM retention interval, and assessed how the load change in visual search affected the allocation of spatial attention and the performance of the spatial WM task. If spatial attention plays a crucial role in WM maintenance and is deprived by visual search, an impairment in the spatial WM performance should be expected.

Study 1

Shape and Spatial Working Memory Capacities are Mostly Independent

Abstract

Whether visuo-spatial WM consists of a common storage resource or of multiple subsystems has been a controversial issue. Logie (1995) suggested that it can be divided into visual (for color, shape, objects, etc.) and spatial (for location) WM. However, a recent study reported evidence against this hypothesis. Using a dual task paradigm, Wood (2011) showed interference between shape and spatial working memory capacities, suggesting that they share a common resource limitation. I re-examined this finding controlling possible confounding factors, including the way to present spatial location cues, task order, and type of WM load to be manipulated. The same pattern of results was successfully reproduced, but only in a highly powered experiment ($N = 90$), and therefore the size of interference was estimated to be quite small ($d = 0.24$). Thus, these data offer a way to reconcile seemingly contradicting previous findings. On the one hand, some part of the storage system is genuinely shared by shape and spatial WM systems, confirming the report of Wood (2011). On the other hand, the amount of the overlap is only minimal, and therefore the two systems should be regarded as mostly independent from each other, supporting the classical visuo-spatial separation hypothesis.

It is well accepted that WM is separated into two systems, namely, phonological (the phonological loop) and visual information storages (the visuo-spatial sketchpad; Baddeley & Hitch, 1974). More controversial is the next assumption that the latter can be further divided into two substructures for visual (colors, shapes, object etc.) and spatial (location) information processing (Logie, 1995), which are usually referred as visual and spatial WM, respectively.

Evidence for this visuo-spatial separation hypothesis has been mixed so far (Luck, 2008). On the one hand, dual task experiments have provided some supportive data. In a typical dual task paradigm, a cognitive task is inserted during the retention interval of a WM task, thus participants have to perform the task and WM maintenance simultaneously. Studies found that the interference between the two tasks became significantly larger when they were related to the same domain (e.g. visual task and visual WM) than when they were related to different domains (Logie & Marchetti, 1991; Tresch et al., 1993; Woodman et al, 2001; Woodman & Luck, 2004). For example, Tresch et al. (1993) found that spatial WM performance was selectively disrupted by a movement discrimination task (i.e. a spatial cognitive task) but not by a color discrimination task (i.e. a feature-based visual cognitive task), whereas the opposite pattern of results was obtained for a shape WM task.

Other studies have suggested that a more nuanced argument might be required for this issue. For example, Wheeler and Treisman (2002) hypothesized that keeping spatial information may not be necessary for maintaining simple features (e.g. "blue" or "triangle") but critical for conjunctive objects (e.g. "blue triangle"; see, however, Zhang et al., 2012). Furthermore, using a change detection task in which the test display was either exactly the same as the memorized one or differed from it in one item, Jiang, Olson, and Chun (2000) reported that performances of simple feature WM tasks (i.e. color or shape) were impaired when item locations were changed between to-be-remembered and to-be-matched stimuli, even though the spatial information was totally task-irrelevant. Although these studies did not directly test the visuo-spatial WM separation hypothesis, they suggested that the proposed dichotomy might be rather simplistic and further investigations were required.

Wood (2011) tackled this problem by investigating the dual task paradigm again, but now in a thoroughly systematic way. In addition, he investigated the consequences of directly combining two WM tasks. This was a notable attempt, since the majority of the previous studies that had utilized the dual task paradigm had only focused on the interference between a WM and a *cognitive* task (e.g. a movement discrimination task; Tresch et al. 1993), which does not examine the interferences between two WM tasks and therefore might not be a direct test of the visuo-spatial separation hypothesis. In contrast, Wood (2011) combined spatial WM tasks with various types of visual WM tasks with the following basic design. White dots appeared on a computer screen at the beginning of each trial, and participants were requested to remember their locations. Next, items with simple color, shape, or conjunctive features were presented, and participants had to remember their identities, too. After a brief blank, a test array was presented, which could be matched with either the spatial WM locations or the visual WM items that were remembered previously. In most of the experiments, the so-called "single probe" task was adopted to test visual WM, where only one to-be-matched item is presented on the test display. The number of to-be-remembered locations and items were manipulated to examine whether and when interference occurred between the two domains.

Despite his effort for an inclusive examination, the results of Wood (2011) only added further complications to the issue. In Experiment 2, he found that increasing the number of spatial cues did not disrupt the performance of the *color*, but did interfere with the *shape* and *object* (color-shape conjunction) tasks. No previous theories and studies are fully consistent with these new data. Firstly, these data clearly contradict the traditional hypothesis of visuo-spatial WM separation, which would have predicted no interference between visual (including shape) and spatial WM (Tresch et al., 1993; cf. Woodman et al., 2001). Secondly, based on the theory of Wheeler and Treisman (2002), overloading spatial WM would have been predicted to deplete the capacity for spatial information maintenance, and therefore interfere with object but not simple feature (e.g. shape) WM. On the other hand, the data of Jiang et al. (2000) would have suggested that spatial WM load would generally affect the visual information maintenance and therefore interact with *both* shape and color WM.

What are the causes of these discrepancies? The first possibility is the differences in task designs, especially between the change detection and single probe tasks. Wood (2011) reported that the interference between color (i.e. a feature) and spatial WM was found only in the change detection, but not in the single probe task. He therefore speculated that in the change detection task, but not in the single probe task, spatial configural information is employed to retain not only spatial, but also visual WM including simple features. In accordance with this hypothesis, Jiang et al. (2002) utilized the change detection paradigm and observed impairments *even* in feature WM performance (i.e. color and shape) when the locations of items were changed during a trial, lending some credibility to the argument. This is, however, not sufficient to account for the interference between shape and spatial WM found in Wood (2011), because the interference was detected not only in the change detection, but also in the single probe task.

In order to reconcile the shape-spatial WM interference reported by Wood (2011) with the previous literature, the current study tried to replicate this finding while controlling some possibly confounding factors observed in the original study. My hypothesis was that these factors might have caused the discrepancy, and therefore a clear conclusion could be obtained if they were fully controlled. The first factor was related to a specific methodological detail Wood adopted, which has already been discussed in some previous studies (Woodman & Luck, 2001; Lecerf & Ribaupierre, 2005). That is, since multiple white dots appeared simultaneously on the computer screen in Wood (2011), the participants might have encoded them as *a shape* formed by these white dots rather than separate *spatial locations*. If this was the case, the observed shape-spatial interference could be interpreted as having occurred between two shape WM tasks. I examined this possibility in Experiment 1a, 1b, and 1c. Next, I also examined the effect of task order (Experiment 2) and types of WM load to be manipulated (Experiment 3). These factors were not, or only minimally manipulated in the original study. To foreshadow the results, none of the controls altered the results. Moreover, no statistically significant evidence of between-domain interference was found in any of these experiments, seemingly disconfirming the observations of Wood (2011). Importantly, however, I found a very small, but consistent trend of interference in all experiments regardless of the different settings, suggesting the obtained null results were simply due to under-powered designs. Therefore, I conducted an omnibus test including four of these experiments and found a small, but statistically significant effect. I also conducted another replication following the design of Wood (2011) more precisely (Experiment 4), in which I collected data from 90 participants to sufficiently increase statistical power. A significant effect of interference was observed again, but its effect size remained to be quite small. I concluded that, although there was an overlap between spatial and shape WM processing, the size of this effect was small, and therefore the two systems should be regarded as mostly independent from each other.

Experiment 1

The purpose of Experiment 1a, 1b, and 1c was to test whether the results of Experiment 2 in Wood (2011) were due to the specific methods that the study adopted for the spatial WM cue presentation or data analysis. Sequential cue presentation was used in Experiment 1a and 1b, and simultaneous cue presentation in Experiment 1c. I examined the interaction between task type and load manipulation as a measure of interference in all three experiments.

Experiment 1a

Methods

Participants. Thirty volunteers (male: 15; female: 15; mean age: 19.93 years, SD: 2.00 years) participated in the experiment. They provided informed consent before commencing the experiment and were compensated monetarily.

Stimuli and Procedure. All stimuli were presented on a black screen of a 17 inch CRT monitor, and E-prime 2.0 (Psychology Software Tools, Inc., Sharpsburg, PA, USA) was used to program the experiment. The viewing distance was about 60 cm.

At the beginning of a trial, 2 alphabet letters (white, bold, and 45 point Courier New font) were randomly selected and presented for 1,000 ms at the center of the screen. Participants had to pronounce these letters repeatedly for articulately suppression until they responded to the test array (see below), in order to prevent the spatial and shape stimuli from being verbalized. To confirm if participants correctly followed this instruction, I recorded their voices all through the experiment by a voice recorder. Participants were informed about this recording procedure beforehand. After the letter presentation, the word “Ready” (white, bold, and 45 point Courier New font) appeared for 500 ms at the center of the screen, followed by a 500 ms blank and then a spatial memory array.

Unlike Wood (2011), the spatial memory array was presented in a sequence. A 5 × 5 grid (width 17.6° × length 14.7°) with white borders appeared for 400 ms at the center of the screen, and consecutively white dots (2.2° × 2.2°) were randomly presented one by one, each for 300 ms, in one of the cells in the grid. The white dots in one trial never appeared in the same cell.

There was no interval between dot presentations, thus the entire presentation time changed according to the set size of the memory array; they were 300, 900 and 1,500 ms for the set size 1, 3, and 5, respectively. Participants had to remember all locations, but not the order of presentation. This spatial memory task was followed by a 800 ms blank and the shape memory array (Figure 1-1A).

The shape memory array consisted of 4 white shapes randomly selected from 7 distinguishable items (star, square, pentagon, triangle, diamond, spiral and cross, see Figure 1-1D), all of which had a size of 3.2° × 3.2°. They remained on the screen for 500 ms. The locations were fixed on the corners of a width 10.1° × length 6.1° rectangle appearing on the center of the screen. The participants had to remember the shapes but not their locations. After the shape memory array, the word "Test" (white color, bold, 45 point Courier New font) appeared for 1,000 ms, and was followed by the memory test.

Two different versions of WM test were used; that is, one for the spatial and another for shape memory, each occurring with a probability of 50%. Note that participants had to retain both spatial and shape information in all trials, since the selection of test type was totally random. For testing spatial WM, a white dot appeared in one of the 5 × 5 grid cells. In half of trials (i.e. 25% of all trials), the dot appeared at one of the locations where the to-be-memorized items had been presented previously (the same condition), and in one of the remaining locations in the rest of trials (the different condition). For assessing shape WM, a shape was selected from the aforementioned 7 shapes (see Figure 1-1D) and presented at the center of the screen. It matched with one of the to-be-memorized shape items in half of the trials (the same condition) but not in the rest (the different condition). In both versions, participants had to answer whether the test item matched with one of the items retained in memory, by pressing the "f" or "j" key on the keyboard (the key-response correspondence was counterbalanced across participants). The test item remained on the screen until the response. A 300 ms blank was inserted as inter-trial interval before the next trial started.

The experiment comprised 30 blocks, each of which contained 12 trials, thus the total number of trials was 360. At the end of each block, accuracy rates of spatial and shape memory test were presented on the monitor. Participants conducted 2 practice blocks with trial-by-trial accuracy feedback before starting the experiment.

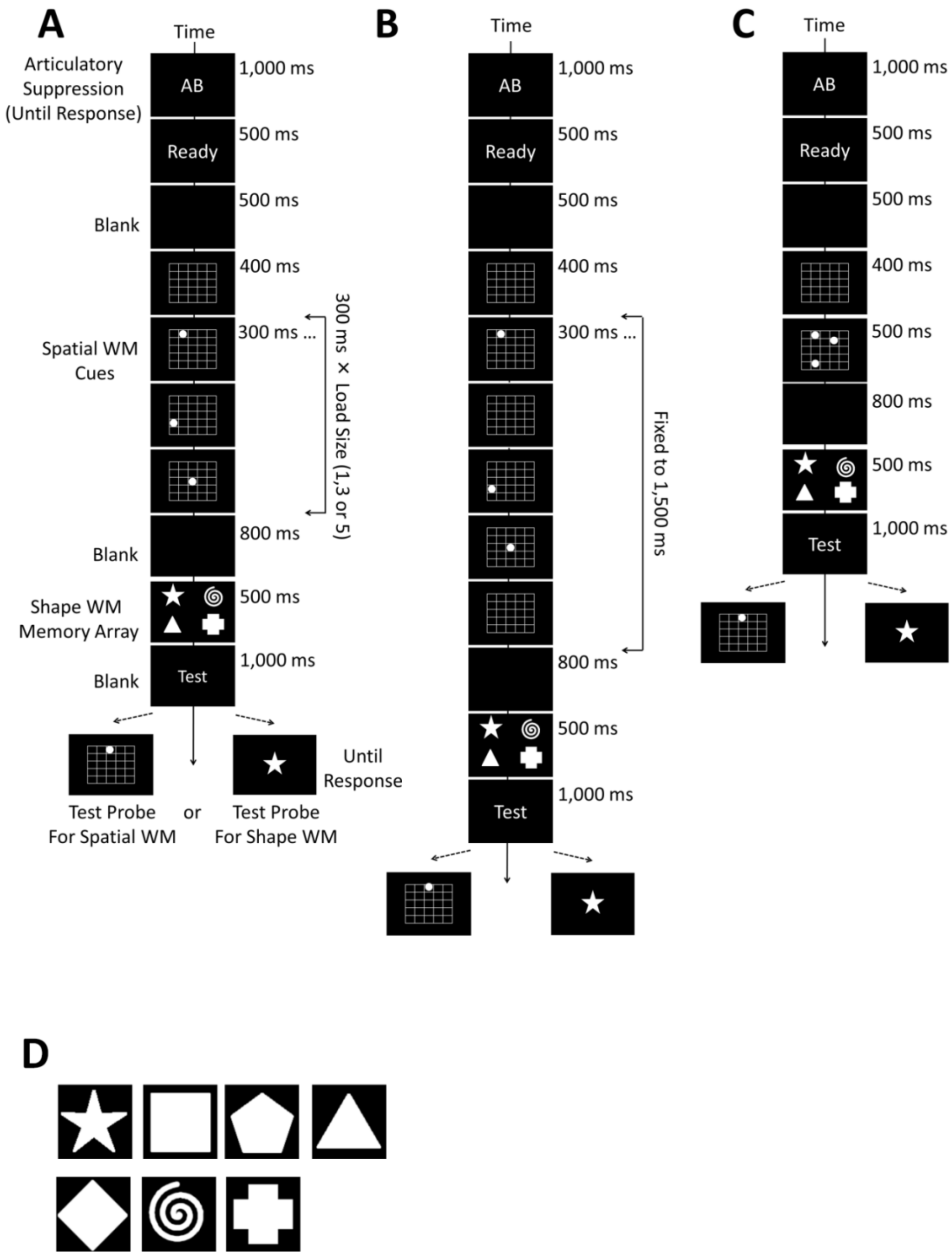

Figure 1-1. Schematic diagrams of the experimental procedures used in Experiment 1a (A), 1b (B) and 1c (C). In all experiments, a trial consisted of the instruction of articulatory suppression, spatial WM memory cues, first blank, shape WM memory array, second blank, and the test probe. Spatial WM was tested in the half of trials, and shape WM in the rest of trials. The load size of spatial WM randomly changed from 1, 3 to 5, but that of the shape WM was fixed to 4. The only difference between Experiment 1a and 1b was the way to present spatial WM memory cues. The total time to present spatial WM cues changed in accordance with the number of the load in Experiment 1a, whereas fixed to 1,500 ms in Experiment 1b. Figure (D) shows the shape stimuli which were used for the shape WM task in Experiment 1a, 1b, 1c, 2, and 4.

Results and Discussion

The results of Experiment 1a showed no evidence of interference between shape and spatial WM. Whereas higher spatial WM load significantly impaired the spatial WM score, it did not affect the shape WM performance (Figure 1-2A). I conducted a within-subject ANOVA on the accuracy data with the two factors, spatial WM load size (1, 3, or 5) and test type (spatial or shape). In addition to a significant main effects of spatial WM load size and test type ($F(2, 58) = 25.63$, $p < .001$, $\eta_p^2 = .47$, $F(1, 29) = 24.03$, 24.03, $p < .001$, $\eta_p^2 = .45$, respectively), the interaction between the two factors was also significant ($F(2, 58) = 16.79$ $p < .001$, $\eta_p^2 = .37$). Post hoc analyses showed that, as spatial WM load increased, accuracy in the spatial WM task decreased significantly (92.8%, 85.7%, and 79.3% for the load1, 3, and 5, respectively; for each difference, *ps* < .001), but shape WM performance did not (80.1%, 79.0%, and 78.8% for the load1, 3, and 5, respectively. *ps* >.995 for the difference between each load size.). Finally, note that the insensitivity of shape WM score to the change of spatial WM load was apparently not due to a floor effect, because the mean performance in all conditions (around 80%) was far better than what would have been expected based on random guesses (50%).

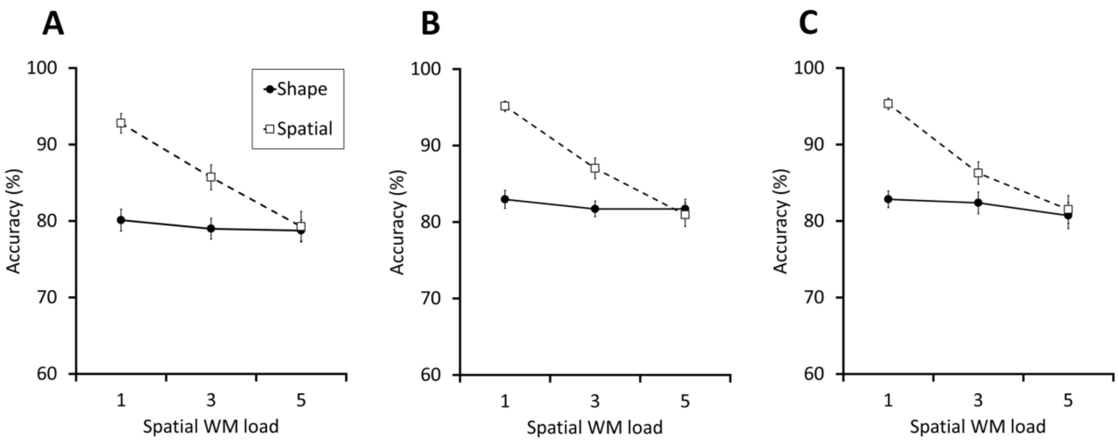

Figure 1-2. The results for Experiment 1a (A), 1b (B) and 1c (C). The broken lines with empty squares and the solid lines with filled circles indicate the accuracy (% correct) of the spatial and the shape WM test trials, respectively. In all experiments, as the spatial WM load size increased, the performance of the spatial WM clearly decreased; the shape WM performance were, however, almost constant. The error bars indicate the standard errors of the mean.

Experiment 1b

The procedure of Experiment 1b was almost the same as Experiment 1a, except that it adopted an alternative way to present the spatial cue sequence. In this experiment, the presentation interval was fixed to 1,500 ms (Figure 1-1B). This procedure eliminated the influence of the difference of interval length between conditions, and made it possible to test more precisely whether the consumption of spatial WM capacity disrupted the shape WM processing.

Method

Participants. Thirty-three volunteers (male: 18; female: 15; mean age: 19.53 years old, SD: 1.76) participated. They provided informed consent before the experiment and were compensated monetarily.

Stimuli and Procedures. The procedure of Experiment 1b was different from Experiment 1a only in the way spatial WM cues were presented. The total duration of spatial cue presentation was fixed to 1,500 ms regardless of the load size. The presentation period was divided into 5 time slots, each of which lasted 300 ms. The appropriate number of slots (1, 3, or 5) was randomly chosen according to the load condition, and spatial memory cues (white dots) were presented at the selected slots (Figure 1-1B).

Results and Discussion

Replicating Experiment 1a, Experiment 1b again showed an absence of interference between spatial and shape WM. I conducted a within-subject ANOVA on accuracy with the two factors spatial WM load size (1, 3, or 5) and test type (spatial or shape; Fig 1-2B). The main effects of spatial WM load size and test type were significant ($F(2, 64) = 50.10$, $p < .001$, $\eta_p^2 = .61$, $F(1,32) = 29.49$, $p < .001$, $\eta_p^2 = .48$, respectively). In addition, the interaction between the two factors was also significant ($F(2, 64) = 23.29$, $p < .001$, $\eta_p^2 = .42$). Post-hoc analyses showed that, as spatial WM load increased, the accuracy in the spatial WM task decreased significantly (95.1%, 87.1%, and 81.0% for load 1, 3, and 5, respectively, for each difference, *p*s < .001). By contrast, the accuracy did not decrease in the shape WM task (82.9%, 81.7%, and 81.7%, for load 1, 3, and 5, respectively. $p = .80$, $p = .83$, and *p*s > .995 for the difference between load 1 - 3, 1 - 5, and 3 - 5, respectively).

Experiment 1c

In contrast to the first two experiments, spatial location cues were presented simultaneously for 500 ms in Experiment 1c (Figure 1-1C). The rest of the procedure remains exactly the same.

Method.

Participants. Twenty-one volunteers (male: 8; female: 13; mean age: 21.0 years old, SD: 3.28) participated. They provided informed consent before the experiment and were compensated monetarily.

Stimuli and Procedures. The only change from the procedures of Experiment 1a and 1b to 1c was that the spatial WM cues were presented simultaneously for 500 ms (Figure 1-1C). The rest of the procedure remained exactly the same as in the two preceding experiments.

Results and Discussion

The results of Experiment 1c proved that the cue presentation method is not the critical factor determining the between-domain WM interference (Figure 1-2C). Again, a within-subject ANOVA on accuracy was conducted with the two factors spatial WM load size (1, 3, or 5) and test type (spatial or shape; Figure 1-2C). Significant main effects of spatial WM load size and test type were confirmed ($F(2, 40) = 30.06$, $p < .001$, $\eta_p^2 = .60$, $F(1,20) = 33.15$, $p < .001$, $\eta_p^2 = .62$, respectively). Critically, the interaction between the two factors reached significance ($F(2, 40) = 14.60$, $p < .001$, $\eta_p^2 = .42$. Post-hoc analyses also showed the same results as the preceding two experiments. Spatial WM load increase significantly impaired the spatial WM task accuracy (95.3%, 86.3%, and 81.5% for load 1, 3, and 5, respectively, for the comparison between load 1 - 3, 1 - 5, *p*s < .001 and 3 - 5, $p = .008$). The accuracy of shape WM task, however, was not affected by the load manipulation (82.9%, 82.4%, and 80.7%, for load 1, 3, and 5, respectively. $p > .995$, $p = .72$, and $p = .932$ for the difference between load 1 - 3, 1 - 5, and 3 - 5, respectively).

In sum, Experiments 1a, 1b, and 1c collectively provided results that were inconsistent with those of Wood (2011), showing no interference between shape and spatial WM performance and therefore suggesting that the storage resource was not shared between the two WM domains. In addition, since the data showed the same trend across the three experiments regardless of the spatial WM cue presentation method, the simultaneous presentation of spatial WM cues adopted in Wood (2011) was not the cause of the discrepancy.

Experiment 2

The objective of Experiment 2 was to examine another possible confounding factor, namely the effect of task order, which was fixed (i.e. spatial then shape) in both Wood's (2011) previous experiments and Experiment 1 of the current study. Thus, in this new experiment I tested whether the same pattern of results as in Experiments 1a, 1b and 1c could be observed even when the task order was reversed (i.e. shape then spatial).

Method

Participants. Twenty-five volunteers (male: 9; female: 16; mean age: 21.40 years old, SD: 3.50) participated. They provided informed consent before the experiment and were compensated monetarily.

Stimuli and Procedures. The procedure of Experiment 2 was identical to that of Experiment 1b except that the order of the spatial and shape WM item presentation was reversed (Figure 1-3A).

Results and Discussion

Experiment 2 replicated the absence of interference between shape and spatial WM systems, regardless of the order of shape and spatial WM task assignments (Figure 1-4A). Again, I conducted a within-subject ANOVA with the two factors spatial WM load size (1, 3, or 5) and test type (spatial or shape). The main effect of load size, F (2, 48) = 12.63, $p < .001$, $\eta_p^2 = .35$, and test type, $F(1,24) = 127.54$, $p < .001$, $\eta_p^2 = .84$ were both significant. Importantly, the interaction between the two factors was also significant, F (2, 48) = 5.69, $p = .006$, $\eta_p^2 = .19$. Post hoc analyses showed that, as spatial load size increased, the spatial WM task became difficult (accuracy 97.0%, 93.2%, and 88.2% for load 1, 3 and 5, respectively; each difference, except between load 1 and 3, was significant, ps < .001), whereas there was no significant difference in the shape WM task (73.2%, 72.0%, and 71.2%, for load 1, 3, and 5, respectively. $p = .98$, $p = .27$, and $p > .995$ for the each difference between load 1 - 3, 1 - 5, and 3 - 5, respectively.). Moreover, the data suggested that the inversion of task order made the spatial WM task much easier compared to the previous two experiments, probably due to a shorter retention interval. In addition, there might have been a ceiling effect especially in the load 1 and 3 conditions. Thus, the smaller effect size of the interaction observed in the current experiment compared to Experiment1 might be a mere consequence of this ceiling effect.

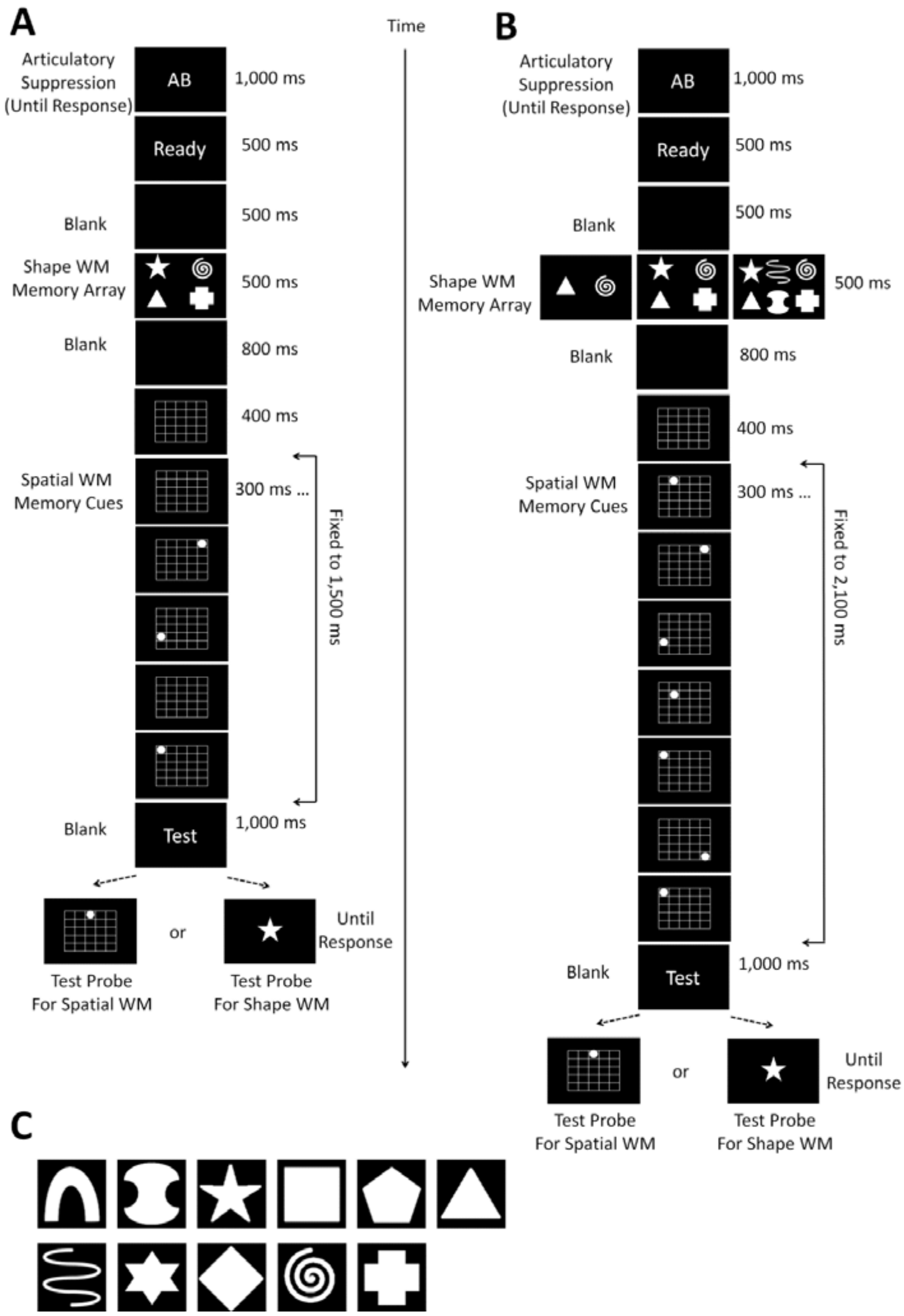

Figure 1-3. Schematic diagrams of the experimental procedure used in Experiment 2 (A) and 3 (B). Experiment 2 was exactly the same as Experiment 1b except that the task order was reversed. In Experiment 3, the load size of shape WM was manipulated (2, 4 and 6) instead of the spatial WM (fixed to 7). Figure (C) shows the shape stimuli which were used for the shape WM task in Experiment 3.

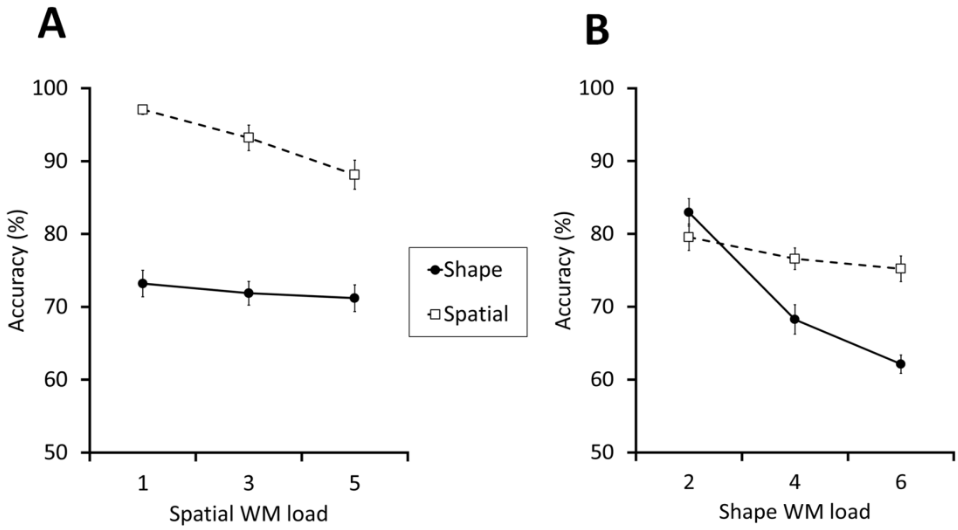

Figure 1-4. The results for Experiment 2 (A) and 3 (B). The broken lines with empty squares and the solid lines with filled circles indicate the accuracy (% correct) of the spatial and the shape WM test trials, respectively. In Experiment 2, although the spatial WM accuracy apparently diminished along with the increment of load size, the shape WM did not. In contrast, the results of Experiment 3 indicated that the shape WM performance sharply fell as the load size increased, whereas the spatial WM did not. The error bars indicate the standard errors of the mean.

Experiment 3

In Experiment 3 I manipulated the *shape*, but not the *spatial* WM load size. The load size for shape WM in the previous experiments in the current study was always set to 4. Thus, one might argue that an alternative interpretation for the results of Experiments 1a, 1b, 1c, and 2 would be that the shape WM impairment was absent because the shape WM reservoir was not completely occupied by the shape items, and therefore there was still room for spatial WM. This account, however, seems unlikely because many studies have proved that a load of 4 items fills up shape WM capacity quite sufficiently (e.g. Cowan, 2001). Nevertheless, I examined this alternative hypothesis, directly manipulating the shape WM load to confirm that there remained no extra space for additional spatial WM.

In addition, the results of Experiment 2 suggested that the shape-first, location-second task order apparently made the spatial WM task easier than in the previous two experiments, and I suspected that it might have produced a ceiling effect (see Figure 1-4A). This would become quite problematic in Experiment 3, because the aim of this experiment was to test the effect of shape WM load on spatial WM performance, and therefore the latter should remain sufficiently sensitive to the effect of interference. Thus, in Experiment 3, I employed the same settings as in Experiment 2 but increased the maximum number of item for spatial WM from 5 to 7.

Method

Participants. Twenty-two volunteers (male: 9; female: 13; mean age: 21.55 years old, SD: 3.51) participated. They provided informed consent before the experiment and were compensated monetarily.

Stimuli and Procedures. The procedure of Experiment 3 was entirely the same as Experiment 2, except for the load size manipulation (Figure 1-3B). The shape WM load changed among 2, 4, and 6, and that for spatial WM was always fixed to 7. In previous experiments, the shapes were selected from 7 items, but I added 4 more alternatives in Experiment 4 (i.e. eleven in total; see Figure 1-3C), because the maximum load size now increased to 6. When the load size was 4, the locations of presentation on the screen were the same as the previous experiments. When it was 2, the two shapes were presented at locations 5° horizontally right or left from the central fixation. Finally, when it was 6, the locations of 4 shapes were the corners of a width 13.1° × length 6.1° transparent rectangle appearing on the center of the screen, and the remaining 2 shapes were presented at the midpoint of the top and bottom sides of the rectangle (i.e. vertically 3.05° up and down from the fixation).

Results and Discussion.

Experiment 3 confirmed again the absence of the shape-location interference in WM regardless of which load size was manipulated (Figure 1-4B). I conducted a within-subject ANOVA on the accuracy, with the two factors shape WM load size (2, 4, or 6) and test type (spatial or shape). In addition to the significant main effects of shape WM load size and test type, (F (2, 42) = 49.14, p < .001, η_p^2 = .70, F(1,21) = 9.64, p =.005, η_p^2 = .31, respectively), the interaction between the two factors reached significance, F (2, 42) = 25.36, p < .001, η_p^2 = .55. Post hoc analyses showed that, as the shape load size increased, the shape WM performance was more and more impaired (83.0%, 68.1%, and 62.1% for load 2, 4 and 6, respectively; for the difference between load 4 - 6: p = .01 and for others: ps < .001), whereas there was no significant difference in spatial WM performance (79.5%, 76.6% and 75.2%, for load 2, 4 and 6, respectively. p = .33, p = .20, and p = .98 for the each difference between load 2 - 4, 2 - 6, and 4 - 6, respectively.).

Thus, my data so far suggested no interference between the two working memory systems, being inconsistent with the findings in Wood (2011). Importantly, however, there was a small, but consistent tendency for the change in the WM load to slightly impair the other, load-unrelated WM performance (i.e. shape WM task in Experiment 1 to 3, and spatial WM in Experiment 4; see Figures 1-2A, 1-2B, 1-2C, 1-4A and 1-4B), even though they did not reach statistical significance in each separate experiment. Since the trend was always in the same direction, I suspected that these null results might have been simply due to statistically underpowered designs. Therefore, I additionally conducted a mixed 4 x 3 x 2 ANOVA on the pooled data across Experiment 1a, 1b, 1c, and 2. Experiment 3 was excluded because it adopted different ways of load manipulation. Data from 109 participants were included. The factors were experiment (i.e. Experiment 1a, 1b, 1c, or 2; between-subject), spatial WM load (1, 3, or 5; within-subject) and test type (spatial or shape; within-subject). This additional analysis revealed a small, but statistically reliable between-domain interference. As in the separate analyses, a significant interaction between spatial WM load and test type was found (F(1.87, 196.71) = 54.97, p < .001, η_p^2 = .34). Also, post-hoc analyses again showed a decrement of spatial WM as a function of the spatial WM load increase (95.1%, 88.1%, and 82.5% for load 1, 3, and 5, respectively. *ps* < .001 for each difference between the load sizes). In addition and most critically, the shape WM performance showed a statistically significant change between load 1 and 5 conditions (79.8%, 78.7%, and 78.1% for load 1, 3, and 5, respectively; p = .27, d = 0.16, p = .045, d = 0.24, and p > .995, d = 0.086, for the difference between load 1-3, 1-5, and 3-5, respectively). Thus, there was a small but significant performance impairment in the load-unrelated task, suggesting that spatial and shape WM share, if only to a small extent, a part of their storage systems.

It should be noted that the procedure of Experiment 1-3 lacked the zero load condition that was included in the original study of Wood (2011). This absence of base-line condition prevented this study from examining the amount of interference that was produced by performing the dual task itself (i.e. performance difference between single and dual task). Wood (2011) called this index the "dual task interference", and used it for examining whether shape and spatial WM systems share their resource. In this sense, my previous experiments did not replicate the original study. Moreover, although my experiments tested whether increase of load size in one WM task decreased performance of the other, this design has a fundamental problem. Strictly speaking, the absence of effect is not enough to affirm the absence of interference, according to the principal of testing null hypothesis. For this reason, I replicated the same procedure as Wood (2011) in the next experiment, involving zero-load condition, in order to assess robustness of the small shape-spatial WM interference that was observed by the comprehensive analysis.

Experiment 4

In Experiment 4, I examined the robustness of the small interference effect observed in the abovementioned omnibus analysis. This time I used a design which followed that of Wood (2011) more precisely. The original study differed from my previous experiments in terms of that (1) it included zero load conditions, (2) it manipulated spatial and shape WM loads within the same experiment, and most critically (3) it calculated a measure of interference called "combined dual-task interference" with the following equation;

> Combined dual-task interference = [(% correct on color/shape/object memory task when performed alone) – (% correct on color/shape/object memory task when performed concurrently with spatial memory task)] + [(% correct on spatial memory task when performed alone) – (% correct on spatial memory task when performed concurrently with color/shape/object memory task)].

I adopted all these factors in Experiment 4. The only difference from the original study was the way to present spatial WM cues, which were shown simultaneously in the original but sequentially in the current experiment. Note that my Experiment 1 already showed that this difference was irrelevant for the results. I collected data from 90 participants to achieve a sufficiently high statistical power to detect any subtle effects. Assuming the abovementioned combined dual-task interference as a key measurement, a sample size of 90 was calculated to be sufficient to detect a relatively small effect size (assuming Cohen's d = 0.3) with a 80% statistical power in a two-tailed paired t test.

Method

Participants. Ninety five volunteers were recruited (male: 53; female: 42; mean age: 24.9 years old, SD: 7.63), but data from five participants were discarded because they showed performance below the chance level (50%) in one of the conditions. Consequently, data of 90 participants were used. They provided informed consent before the experiment and were compensated monetarily.

Stimuli and Procedures. Following Experiment 2 of Wood (2011), I manipulated both spatial and shape WM load within experiment; the spatial WM load was set to 0, 3, or 9 locations and shape load was 0 or 4. The basic design was similar to Experiment 1b except that the total time period for spatial cue presentation was fixed to 2,700 ms. The period was divided into 9 slots, each of which lasted 300 ms. The appropriate number of slots (0, 3, or 9) was randomly chosen according to the load condition, and spatial memory cues (white dots) were presented at selected slots (Figure 1-5A). When the shape load was 0, four "filler" objects were presented to equalize the perceptual demand across conditions. When spatial load was 0, only the grid was presented with no cues. The rest of the procedure remained exactly the same as Experiment 1b.

Results and Discussion

I firstly analyzed my data following the methods described in Wood (2011). In sum, I successfully replicated most of the results reported in the study. First, a within-subject ANOVA was conducted for shape WM performance and showed a small but significant main effect of the spatial WM load increase ($F(2, 178) = 9.36$, $p < .001$, $\eta_p^2 = .095$). Second, another ANOVA was done for the spatial WM scores with the factors spatial (3 and 9) and shape WM load size (0 and 4), and revealed significant main effects of spatial ($F(1, 89) = 136.90$, $p < .001$, $\eta_p^2 = .61$) and shape WM load ($F(1, 89) = 977.07$, $p < .001$, $\eta_p^2 = .92$). I only failed to replicate an interaction between these two load factors ($F(1, 89) = 1.76$, $p = .19$, $\eta_p^2 = .019$), which had been significant in the original study. These results are depicted in Figure 1-5C together. Third, the "combined dual-task interference" was calculated following the equation introduced in the Introduction section of the current experiment, and data was compared between 3 and 9 spatial WM load sizes using a two-tailed paired *t*-test (Figure 1-5B). A small but significant difference was found ($t(89) = 2.31$, $p = .023$; Cohen's $d = 0.24$), which was also a successful replication of Wood (2011). Thus, the results of Experiment 4 demonstrated the robustness of the between-domain interference, confirming the report of Wood (2011). In addition, the effect size was very small, suggesting that separate analyses in Experiment 1a to 3 did not have sufficient power to detect it.

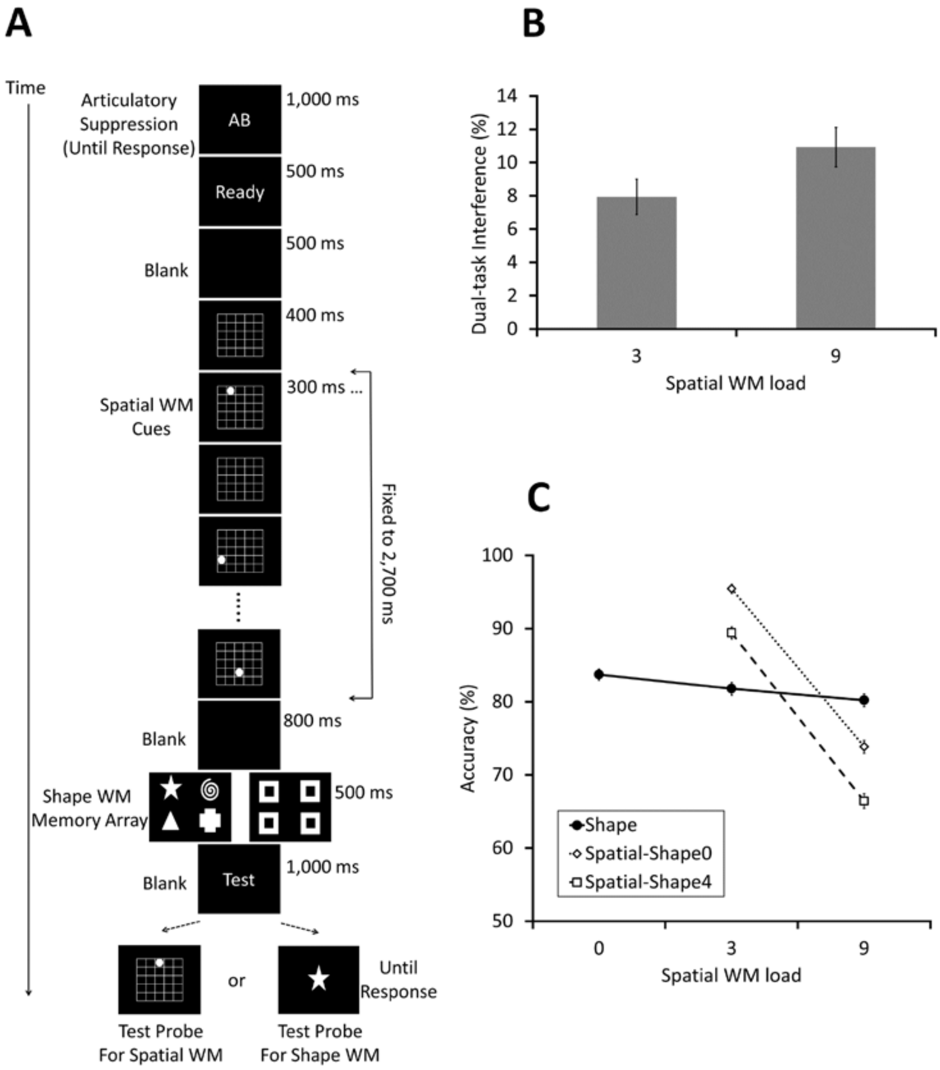

Figure 1-5. The experimental procedure (A) and results (B, C) for Experiment 4, which was an exact replication of Experiment 2 of Wood (2011), except that the spatial cue presentation was conducted sequentially instead of simultaneously. The load size of spatial WM randomly changed from 0, 3, to 5, and that of the shape was also manipulated (0 and 4) randomly. Figure 5B depicts the "combined dual task interference" scores, which were calculated following Wood (2011) (see text for the details), as a function of spatial WM load. On the other hand, Figure 5C shows the whole structure of the data, as I did in other experiments of the current study. In Figure 5C, the dotted line with empty diamonds and the broken line with empty squares show the accuracy (%) correct of the spatial WM test trials when the shape WM load size was 0 and 4, respectively. The solid line with filled circles indicate the accuracy of the shape WM test trials. Figures (B) and (C) illustrate small but significant between-domain interference.

General Discussion of Study 1

The objective of the current study was to investigate the validity of the hypothesis that visual and spatial WM have two independent, separated storage systems. For this aim, I re-examined the results of the shape-location dual task experiment reported in Wood (2011), which provided putative evidence against the hypothesis. I considered several possibly confounding factors detected in the original study to account for the discrepancy. I tested whether the cue presentation procedure (Experiment 1a, 1b, and 1c), order of tasks (Experiment 2), and the type of working memory that was manipulated (Experiment 3) affected the interference effect. None of these factors had impact on the results, thus excluding the possibility that the results of Wood (2011) were confounded with some uncontrolled factors. However, I also failed to replicate the findings of Wood (2011) in all experiments. When each experiment was separately analyzed, I found no evidence of shape-location interference. I found, however, an insignificant, but consistent trend of mean accuracy impairment in the load-unrelated WM tasks, which suggested the possibility that the experiments had too little power to detect the target effect. Therefore, I first re-analyzed my own data combining those from Experiment 1a, 1b, 1c, and 2, and obtained a statistically significant effect in the load-unrelated task. Moreover, an additional, direct replication of Wood (2011) with a sufficiently large data set (N = 90) confirmed the effect again, suggesting that the interference truly exists, but is so small that it could not be detected in separate experiments due to low statistical power.

Then, the critical question is how these results should be interpreted in the context of the visuo-spatial WM separation hypothesis. First, it should be noted that the performance interference itself does not guarantee that there is an overlap of storage capacity between spatial and shape WM. The same result might have been obtained due to an increase of non-specific task difficulty that is not specific to working memory storing. For example, Woodman et al. (2001) reported that the visual WM performance was generally deteriorated in a dual task paradigm, because of nonspecific masking or interruption of WM items triggered by the simple stimulus presentation in the alternative task.

In order to obtain preliminary insights on this issue, I conducted two additional experiments with small data sets (N = 30 and 21, respectively). The first experiment tested whether simple presentations of location cue, without posing any spatial WM task, would cause an impairment of the concurrent shape WM task. The setting of Experiment 1b was adopted with the following modifications. Zero, three, or nine spatial location cues were presented, but spatial

WM task was never required (Figure 1-6A). The results showed no statistically significant interference. Moreover, the mean accuracy even improved from load zero to three and nine conditions (84.7, 85.9, and 85.2%, respectively; Figure 1-7A). The second additional experiment examined whether the interference could be caused by attentional processes not involving working memory storing. Participants were required to conduct a visual search task (Figure 1-6B), and asked to press a key if they found the target, after all search items had

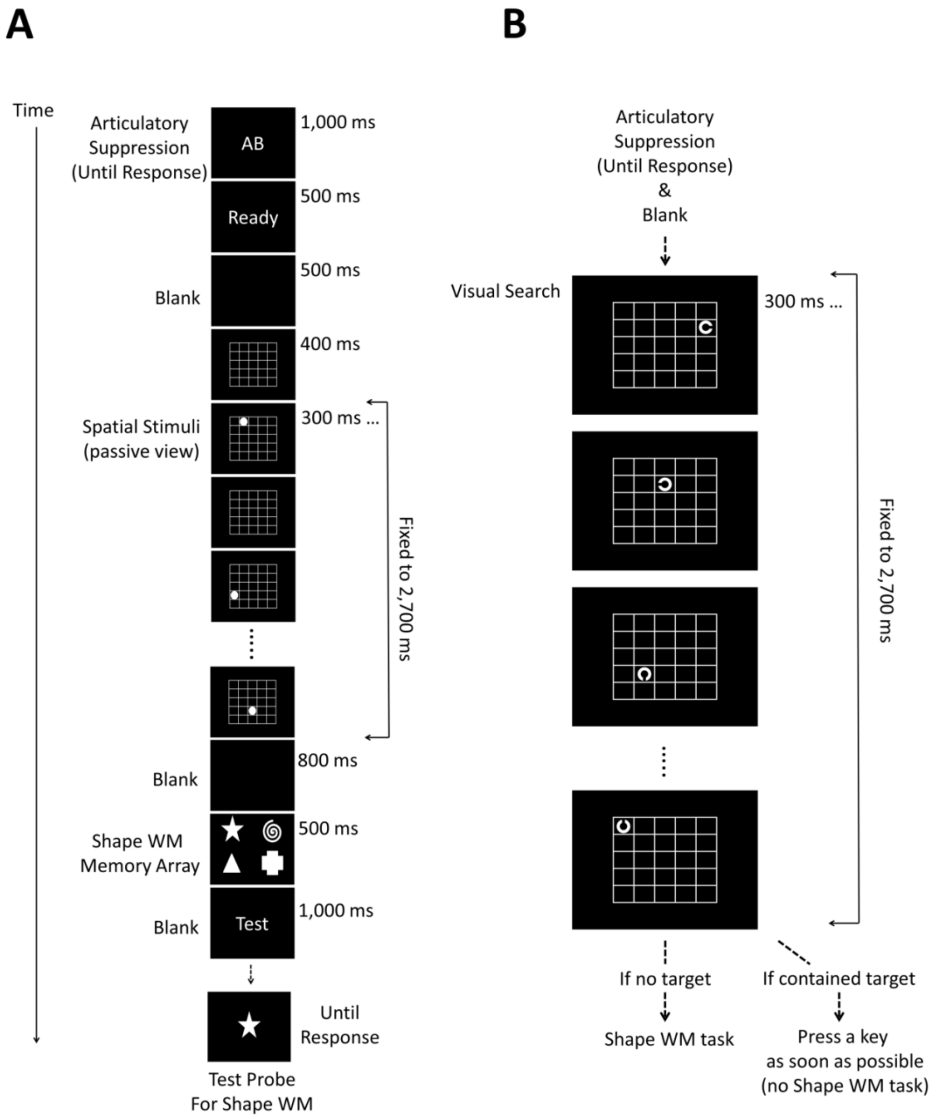

Figure 1-6. Schematic diagrams of the experimental procedure used in additional preliminary experiments explained in General Discussion. The experiment that examined whether perceptual masking caused the interference effect is shown in Figure (A), and the experiment that examined attentional processes in Figure (B; see General Discussion for details).

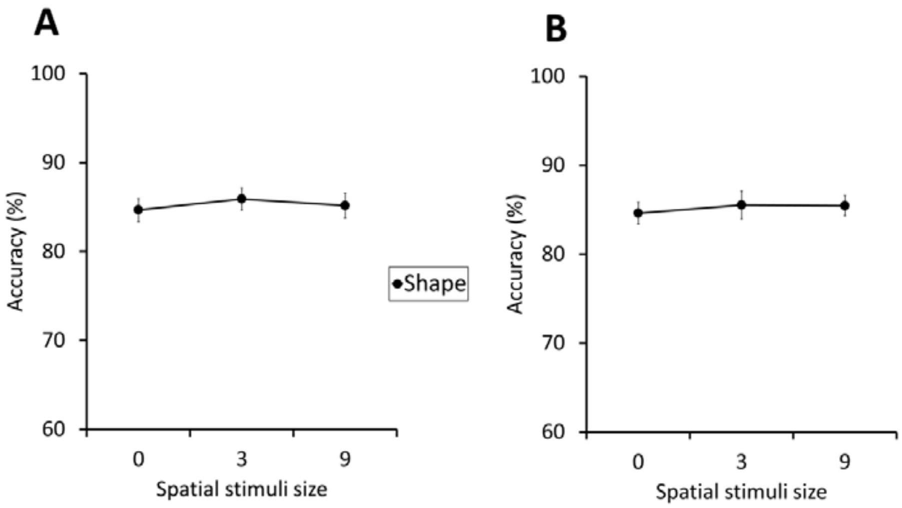

Figure 1-7. The results of additional preliminary experiments discussed in General Discussion, depicting the accuracy (% correct) of the shape WM performance (see General Discussion for details). The error bars indicate the standard errors of the mean. Figure (A) shows the result of the experiment that examined whether perceptual masking caused the interference effect. Figure (B) shows the result of the experiment that examined attentional processes.

appeared (i.e. when the spatial grid disappeared). Search items were Landolt rings and the one that had an open part on the upper side was designated as target, which appeared randomly once in 7 trials. Set size was manipulated among zero, three and nine. The rest of the settings were the same as Experiment 1b. Results showed no significant effect of array size. In addition, a trend of shape WM improvement was observed again as the array size increased (84.8, 85.4, and 85.5% for array size zero, 3, and 9, respectively; Figure 1-7B).

Although the small sample sizes did not allow to draw definite conclusions, the present pattern of results, i.e. improvement of mean accuracy score as the numbers of location cues increased, has not been observed in my previous experiments, where the genuine spatial WM task was required. Thus, I speculated that the mere perceptual masking and attentional processes were probably not the cause of the between-task interference, and therefore the effect was possibly triggered by some processes related to working memory storing, suggesting that the two WM domains have an overlapping storage system.

However, it is also important to point out that the size of the interference was quite small across Experiments 1a to 4, and this observation makes me to hesitate to conclude that the two systems fully share their capacities. Presumably, the most straightforward way for measuring the interference between two storage systems is to test whether the maximum number of items that can be remembered remains the same, regardless of which item dimension is assigned to memorize (Zhang et al. 2012). If two (or more) WM domains have a fully interdependent storage system, then the maximum capacity should be unchanged and limited to the same amount, regardless of which working memory load was manipulated. Woodman and colleagues reported a good example of such examination in the visual domain (Woodman et al., unpublished data; cited in Zhang et al. 2012). They tested whether color and orientation WM shared a common system by comparing the performance between when participants had to remember six color or orientation items and when they were required to memorize three from each category. The results showed no significant difference between two conditions, suggesting that the two memory capacities overlap to a significant degree. Assuming that this type of result is the gold standard to demonstrate a full capacity overlap between WM domains, the small effect size I obtained in the current study seemed insufficient to state that spatial and shape WM systems fully shared their storage systems.

This interpretation might solve some of the disparities observed in previous studies, including Wood (2011). As I have already discussed in Introduction, there has been a profound inconsistency among the previous studies on this issue. On the one hand, some dual task studies supported the distinction between visual and spatial cognitive systems by showing the absence of interference between them (Logie & Marchetti, 1991; Tresch et al. 1993; Woodman et al. 2001; Woodman & Luck, 2004). On the other hand, other researchers proposed alternative hypotheses that conflicted with the idea of simple visuo-spatial separation (Jiang et al., 2000; Wheeler & Triesman, 2002). Finally, the results of Wood (2011) further deepened the problem, since none of the previous theories was consistent with the data. Possibly, one of the reasons for these inconsistent results was that some of the studies were simply underpowered to detect the between-domain interference, as shown in my Experiment 1a to 3.

In conclusion, whereas some parts of shape and spatial WM systems are overlapping, their capacities are mostly independent from each other. Thus, our data support the visuo-spatial WM separation hypothesis proposed by Logie (1995). Moreover, our results were in line with the argument proposed by Wheeler and Treisman (2002). They argued that keeping spatial information is necessary for WM maintenance of conjunctive objects (e.g. "blue triangle"), but not for simple features (e.g. "blue" or "triangle"). However, further research is required to fully resolve the controversy. First, since the original visuo-spatial WM separation hypothesis maintains the independence of spatial WM capacity not only from the feature (e.g. shape) but also the object WM system (Logie, 1995), the object-spatial WM interference should also be examined. Second, Jiang et al. (2000) suggested that storing even simple features needs retention of their spatial relationship, and this seems to be incompatible with the current study. Jiang et al. (2002), however, utilized change detection tasks, the structure and processing of which could be significantly different from the single probe task I employed in the current study. Therefore, this task difference should also be investigated in future research.

Another important concern would be the neural substrates underpinning this functional separation of WM systems. The First candidate would be the prefrontal cortex. Using electrophysiological recordings of neural activity in macaque monkeys, Wilson, Scalaidhe, and Goldman-Rakic (1993) suggested that visual and spatial WM could be separately implemented in the ventro- and dorso-lateral areas of the prefrontal cortex. This hypothesis was further supported by human imaging studies (Courtney, Ungerleider, Keil, & Haxby, 1996; Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998.; cf. Mishkin, Ungerleider, & Macko, 1983). However, many other studies have provided evidence inconsistent with this simple dichotomy (Rushworth, Nixon, Eacott, & Passingham, 1997; Rao, Rainer, & Miller, 1997; Postle, Stern, Rosen, & Corkin, 2000). For example, by utilizing lesion technique, Rushworth et al. (1997) found that the ventral prefrontal area, the inferior convexity in particular, was not important for working memory processing. In addition, Rao et al. (1997) showed that the neural populations in the prefrontal area which correlated with visual or spatial WM could not be separated simply. They found that many neurons showed activity related to both visual and spatial WM maintenance. Finally, Postle et al. (2000) tried to examine the abovementioned separation at the neural level in humans, but failed to replicate previous studies. Thus, this possibility still remains highly controversial. In contrast, the distinction between ventral visual and dorsal spatial pathway in the visual cortex has been largely accepted among researchers (Mishkin et al., 1983). If this visual pathway difference defines the WM separation, it indicated that the capacity limit of WM is generated in each visual processing domain. There has not been, however, yet any direct evidence to connect this pathway difference to the separation between WM domains. Further research is needed to shed light on this issue.

Study 2

Reexamining the Attention Rehearsal Hypothesis of Spatial Working Memory Maintenance

Abstract

It has been argued that the maintenance of spatial WM contents is carried out by sustained activity of selective spatial attention that focuses on the specific locations at which the WM items are presented (Awh et al., 1998). This attention-based rehearsal hypothesis, however, remains controversial (Belopolsky & Theeuwes, 2009; Chan et al., 2009). The current study examined this hypothesis using both behavioral and ERP measures of spatial attention. The behavioral experiment was an approximate replication of previous studies, whereas the ERP experiments further examined whether the retained attention, if it exists, was actively maintained or a mere passive after-effect of the encoding process. As in previous ERP studies, task-irrelevant probes were used to elicit the P1/N1 attention effect. Results showed that spatial attention was allocated to the to-be-remembered locations during the retention period, although this was not reliably detected by the behavioral index. Moreover, attention strength was unchanged even when a visual search task that presumably induced an additional workload was concurrently administered. These data might indicate that an active, top-down, and location-specific maintenance of spatial attention is in fact at work during spatial WM retention, although its functional significance is still not completely confirmed.

Attention is believed to play a critical role in the encoding and maintenance of WM (Awh, et al., 2006). More specifically, Awh and his colleagues proposed the so-called spatial attention rehearsal theory of spatial WM (Awh et al., 1998; Awh & Jonides, 2001), which argues that spatial information in WM is maintained by a persistent activity of spatial attention that is focused on the to-be-memorized spatial location. Putatively, this theory has been supported by three types of evidence. First, cortical regions or networks mediating spatial WM were highly overlapped with those of spatial attention. It has been found that both functions were related to the activation of the fronto-parietal network, which is dominant in the right hemisphere (Awh, Smith, & Jonides., 1995; Ikkai & Curtis, 2011). Second, attention-like facilitative effects on visual processing were observed during spatial WM maintenance. It is well known that spatial attention facilitates the processing of stimuli that appear around the center of its focus (Posner & Cohen, 1984). If spatial attention plays a role in maintaining spatial WM, the same facilitative effect should be detected during spatial WM maintenance. Several studies using behavioral as well as neural measurements have confirmed this prediction (Awh et al., 1998; Awh et al., 2000; Jha, 2002). Finally, it has been shown that deprivation of spatial attention during spatial WM maintenance impaired memory performance, indicating that attention plays a critical role for retaining WM items (Smyth & Scholey, 1994; Smyth, 1996; Awh et al., 1998; Oh & Kim, 2004; Woodman & Luck, 2004). Although these data seem to support the attention rehearsal hypothesis, there are some reasons not to accept it easily, especially regarding the second and third lines of evidence.

Evidence showing the Attentional Facilitation Effect

The facilitative, attention-like effect during spatial WM maintenance was firstly reported by Awh et al. (1998). A letter-like item was presented during a spatial WM retention interval (a “choice probe”, henceforth), and participants were required to identify the shape of this choice probe in addition to the concurrent spatial WM task. The behavioral performance for the probe identification task was improved when the choice probe was presented at the memorized, as compared to other non-memorized locations. Since this facilitative effect closely resembled that of spatial attention, it was considered as evidence that spatial attention was continuously focused on the memorized locations during WM maintenance.

Furthermore, other studies confirmed the same facilitative effect by measuring neural indices of spatial attention. Using an experimental paradigm similar to the behavioral one, Awh et al. (2000) recorded the P1 and N1 ERP components elicited by a task-irrelevant visual probe (an "ERP probe", henceforth), which was presented during the spatial WM maintenance interval. P1 and N1 are commonly observed at posterior electrodes, showing their maximum amplitudes on the sites contralateral to the visual field where stimuli are presented. These ERP components are believed to reflect early perceptual processes of incoming stimuli, and spatial attention amplifies their amplitudes (Mangun, Hillyard & Luck, 1993; Hillyard, Vogel, & Luck, 1998). Awh et al. (2000) compared these ERPs amplitudes between a condition where the ERP probe was presented in the visual field that contained memorized locations (the on-target condition) and a condition where it appeared on the opposite visual field (the off-target condition). The results showed that the amplitudes of P1 and N1 were larger when the probe appeared on the memorized side, indicating the presence of spatial attention in spatial WM maintenance. Moreover, this attention-like ERP effect was replicated by Jha (2002), who also measured probe-evoked P1 and N1 with an additional manipulation of the presentation timing of the ERP probe between the early and late periods during the retention interval. Again, enhanced amplitudes of P1 and N1 were observed in both time ranges, indicating that spatial attention was focused on the memorized locations throughout WM maintenance. Finally, a functional magnetic resonance imaging (fMRI) study also replicated the same attention-like effect, showing that a possibly facilitative effect occurred in the early visual areas (Awh, Jonides, Smith, Buxton, Frank, Love, et al., 1999).

According to these studies, it seems that the attentional facilitation effect during spatial WM maintenance is quite robust, having survived several tests of replication. There are, however, some issues that could still cast a doubt on these findings. First, Belopolsky and Theeuwes (2009) reported that they failed to replicate the attentional benefit reported by Awh et al. (1998). Using almost the same paradigm as the original study, they observed that the response for the choice probe presented at the memorized locations was not faster but rather slower than the response for non-memorized locations. They interpreted this result as an indication of inhibition, and concluded that spatial attention plays no role in spatial WM maintenance.

Furthermore, there seems to be a methodological problem in one of the abovementioned ERP studies. In Awh et al. (2000), the ERP probe was a checker board which subtended the whole right or left hemi-field, and this might have weakened the sensitivity of ERP measurements to correctly detect the attentional effect. For the sake of argument, let us assume that spatial attention is not required to maintain spatial WM and imagine the case that the participant vaguely directed her/his spatial attention to the whole right or left visual field where the memory cue was presented, but with no particular focus on the memorized locations. The ERP probe adopted in Awh et al. (2000) should be able to detect an attentional facilitation effect even in this case. Such an assumption of unfocused attention to the whole visual hemi-field is not so unrealistic in this case, because three memory cues and a test item were all presented on the same hemi-field. Therefore, it was highly probable that participants knew in which field the test item would appear, and they might have been expecting it during the maintenance period. In such situation, spatial attention could be vaguely allocated to the expected hemi-field, even without any significant role to maintain spatial WM locations. It should be noted that the other ERP study on this topic, namely Jha (2002), did not have this methodological problem. Since the ERP probe was not covering the whole hemi-field in this study, the expectancy problem found in Awh et al. (2000) was avoided, and therefore the attentional facilitation effect observed in Jha (2002) could be regarded as direct evidence of the spatial attention allocation during spatial WM maintenance. In summary, only Jha (2002) has provided convincing evidence that spatial attention is allocated precisely to the locations where spatial WM items were remembered. More investigations are needed to confirm this effect.

Evidence showing the Attention Deprivation Effect

It should be noted that even if spatial attention is directed at the to-be-remembered locations, it does not guarantee that it plays a functional role to maintain spatial WM contents. It could be the case that spatial attention is used in the encoding phase of the spatial WM task, and remains there only passively for a certain period of time. Thus, it is necessary to test the causal relationship between attention and WM maintenance by inducing, for example, a deprivation of spatial attention during the retention interval, and test whether it significantly impairs the spatial WM performance. For this purpose, Awh et al. (1998) inserted a color discrimination task during the spatial WM retention interval in order to jumble spatial attention. In one condition, participants were required to identify the color of a small disk, which was presented on the peripheral visual area so that attention needed to be shifted to the target locations (the shifting-attention condition). In another condition, the same color classification task was required, but the size of the disk was large enough to occlude all locations to be memorized, so that participants had no need to shift their attention (the static attention condition). The results showed that the attention shift significantly impaired WM performance, indicating that spatial attention was crucial for spatial WM maintenance. In addition, Oh and Kim (2004) and Woodman and Luck (2004) used dual task paradigms, in which a difficult visual search was inserted during a spatial WM task, and examined whether an interference occurred between these two tasks was examined. The search task was supposed to be sufficiently difficult to induce a serial shift of attention among stimuli until the target was identified (Woodman, Vogel, & Luck, 2001; Woodman & Luck 2003). These studies also found that visual search significantly impaired the spatial WM performance and the size of interference increased as the search set size became larger, providing further evidence for the hypothesis.

These studies, however, are also not free from controversies. Chan et al. (2009) argued that the disruption of the WM performance reported in Awh et al. (1998) was not specifically due to the shift of spatial attention, but rather induced by a general increase of the task demand in the shifting-attention condition. In order to test this claim, Chan et al. (2009) used visual search as the secondary task and equalized the general task demand between the shifting- and static attention conditions by using completely the same stimuli. The only difference between two conditions was whether the search target appeared at the same location as the to-be-memorized spatial WM position (the static attention condition) or different locations (the shifting-attention condition). Surprisingly, they observed no difference in spatial WM performance between the two conditions, and thus argued that spatial attention does not play a crucial role in spatial WM maintenance.

The Current Study

Altogether, the evidence supporting the attention-based rehearsal hypothesis is still small and the results have been mixed. The goal of the current study was to re-examine the behavioral and ERP evidence of the rehearsal hypothesis by focusing on the facilitative attention effect that could prove whether spatial attention is allocated precisely on the memorized positions (Experiment 1), and on the attention deprivation effect that could indicate the functional role of spatial attention in the maintenance of spatial WM (Experiment 2).

Experiment 1 was an approximate replication of previous studies on this topic. Although Awh et al (1999) and Belopolsky and Theeuwes (2009) used almost the same experimental procedure, their results significantly diverged. The exact reason of this discrepancy is unknown, but it is possible that subtle differences in methodology or some innate instability of the effect (e.g. fluctuation of the results due to a relatively small effect size and low statistical power) lead to the divergence. Thus, a replication using approximately the same paradigm is informative. As in the previous studies, an object discrimination task was inserted during the spatial WM retention interval, and response time was compared between the on- and off-target conditions. In addition, the size of area within which both the to-be-memorized locations and the probe item would appear was manipulated, in order to assess the effect of distance between the choice probe and memorized locations. If the attentional facilitation effect gradually spread from the center of the attentional focus to peripheral regions, then the longer the distance became, the weaker the effect should be. To preview the results, no difference in response time between the conditions was observed in any distance conditions, showing a consistency with Belopolsky and Theeuwes (2009). There is, however, the possibility that the behavioral index used in Experiment 1 was not sensitive enough to detect the effect, and therefore I tested whether the result was replicable even when ERP measurements were used.

The goal of Experiment 2 was twofold. Firstly, the attentional facilitation effect was tested again using ERP measurements. This was an approximate replication of the previous ERP studies on this issue (Awh et al. 2000; Jha, 2002). The P1 and N1 ERP components induced by the ERP probes were measured and their amplitudes were compared between the on- and off-target conditions. The possible confound of the expectancy effect observed in Awh et al. (2000) was avoided by using a small white dot as the ERP probe instead of one covering the whole hemi-field.

The second purpose of Experiment 2 was to examine the functional significance of spatial attention for spatial WM rehearsal. As in the previous behavioral study (Awh et al., 1998), a difficult visual search task was inserted during the spatial WM retention interval. Previous research has shown that this type of visual search demands a serial deployment of attention (Woodman, et al., 2001; Woodman & Luck 2003). It was predicted that, if attention plays a crucial role in spatial WM maintenance, the attention deprivation induced by the visual search task should decrease the spatial WM score, especially as the search array size increased. Moreover, the amount of attention allocated to the memorized locations was measured by the P1/N1 components, and the correlation between the deficits in the spatial WM performance and the attention effect detected by ERP was also examined. Specifically, if attention is necessary for WM maintenance, the attentional effect on the ERP indices should remain the same regardless of the attentional demand in the visual search task, given that the WM task was correctly performed. None of the previous studies investigated the attention effects in a dual task paradigm combining a spatial WM and visual search task. However, the use of ERP indices is highly effective in this paradigm, since a dual task is already highly demanding in terms of the task structure, and ERP measurement requires no additional task complexity.

Experiment 1

The purpose of Experiment 1 was to replicate the behavioral experiments of Awh et al. (1998) and Belopolsky and Theeuwes (2009). The differences between the previous studies and the current one were as follows. First, although positions for presenting spatial cues were chosen from fixed slots in the previous studies (108 places in Awh et al, 1999; 36 or 108 in Belopolsky & Theeuwes, 2009), they were completely randomized in the current study. Second, letter-like stimuli were used as the choice probe in the previous studies, whereas letter L and inversed T were used in the current one. Finally, the size of the area in which all the WM cues, WM test-probes and choice probe were presented was manipulated between the whole-field and hemi-field conditions. This comparison was intended to roughly examine the effect of the distance between the WM cue (i.e. the memorized location) and the choice probe.

Methods

Participants. Thirty-three volunteers (male: 16; female: 17; mean age: 20.73 years with SD 2.61 years) participated in the experiment. They provided informed consent before commencing the experiment and were compensated monetarily. The data of 6 participants were excluded because of excessive eye movements (see below for the criteria), thus 27 participants' data were analyzed.

Stimuli and Procedure. All stimuli were presented on a gray screen of a 17 inch CRT monitor. E-prime 2.0 (Psychology Software Tools, Inc., Sharpsburg, PA, USA) was used to program the experiment. The viewing distance was about 60 cm.

The sequence of events is illustrated in Figure 2-1. A fixation cross (0.7° × 0.7°) was presented at the center of the screen throughout a trial. At the beginning of a trial, a memory cue (black square, 1.1° × 1.1°) appeared for 200 ms. Participants had to memorize the exact location of the cue. To prevent verbal coding of locations, memory cue position was randomized in two rectangular regions (width 9.2° × length 13.3°) that were centered 5° to the left and right of the central fixation. During the 3,600 ms retention interval, a choice probe (white "L" or inverted "T", 1.1° × 1.1°) was presented for 200 ms in the rectangular regions. Participants were required to determine as fast as possible which shape was presented, by pressing keys on a standard keyboard (for key-response mapping, see below). A blank between the memory cue and choice probe was randomly selected from 800, 1200, 1600 ms. In 25% of trials, the location of the choice probe was exactly the same as the memorized position (the on-target condition), and in different locations in the remaining 75% trials (the off-target condition). This biased ratio of on-/off-target conditions was set in order to prevent participant from predicting the location of the choice probe. At the end of trial, a test probe (tilted black cross, 1.1°× 1.1°) was presented in the rectangular regions until response. The test probe appeared at the memorized location in 50% of the trials and at a different position (with at least 2° distance from the memorized location) in the remaining trials. Participants had to answer whether the test probe appeared at the memorized position by pressing a key. For this memory task, accuracy was emphasized rather than speed. Fourteen of the participants were instructed to press the "d" or "f" key for the choice task, and to press the "j" or "k" key for the memory task. The key-response mapping was reversed for the rest of participants.

There were two conditions with regard to the size of the area in which stimuli were presented. In the whole-field condition, all stimuli were presented in two rectangular regions (Figure2-1A). On the other hand, in the hemi-field condition, stimuli appeared in either the left or right rectangular region (Figure2-1B).

Each of 64 blocks consisted of 12 trials. At the end of each bock, accuracy rates for the spatial WM and discrimination task were displayed on the screen. The experiment was divided into 2 sessions which were conducted on different days, and the presentation field conditions were administrated in different sessions. The order of stimulus presentation conditions was counterbalanced across participants.

For analysis, trials with ocular artifacts and trials with error responses in the choice probe and spatial WM tasks were discarded. Trials with response times over 3 standard deviations above the mean were also excluded.

Electro-Oculogram Recording and Analysis. In order to exclude ocular artifacts, eye movement was monitored by vertical and horizontal electrooculograms (VEOG and HEOG). Data were recorded with a sampling rate of 500 Hz using a band-pass filter of 0.05 - 100 Hz (AC recording) with Neuroscan SynAmp2 System (Neuroscan Inc., Charlotte, NC, USA) and EasyCap electrodes (EasyCap GmbH, Herrsching, Germany). All electrode impedances were kept below 10 kW. The VEOG was recorded from two electrodes above and below the left eye. The HEOG was recorded from two electrodes placed at the outer sides of the left and right eyes. A bipolar derivation was used for the EOGs. Data were epoched from -100 ms before the memory cue onset until the choice probe onset (i.e. 1000/1400/1800 ms after the memory cue onset). One hundred-millisecond interval prior to the memory cue onset was used as baseline. Trials with eye movement or blinks (HEOG exceeding ±30 μV, VEOG exceeding ±75 μV) in the time range were discarded from analysis. These criteria have been commonly used in studies that need to control eye movements (e.g. Dell'Acqua, Sessa, Toffanin, Luria & Jolicoeur, 2010). One degree of saccard yield approximately 16 μV deflection (Lins, Picton, Berg & Scherg, 1993; Luck, 2005), thus the ±30 μV criterion ensures that eye movement is always less than 2°. The data of 6 participants with rejection rates of 30% or higher were excluded.

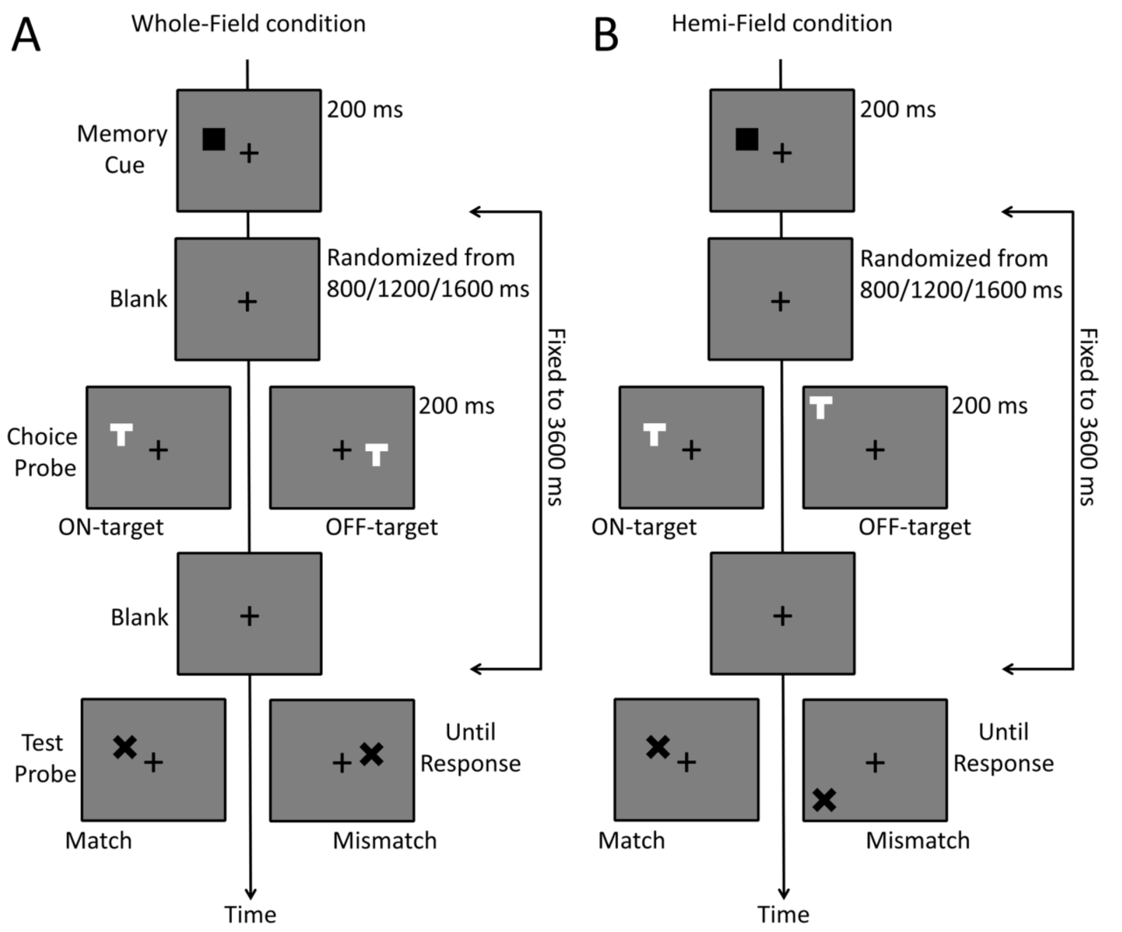

Figure 2-1. Schematic diagrams of the experimental procedure in Experiment 1. A trial consisted of spatial WM memory cues, the first blank, a choice probe, the second blank, and a spatial WM test probe. The number of to-be-remembered location was fixed to one. For the choice probe task, a white L or inverted-T-shape was presented during the retention interval of spatial WM, and participants were required to identify the shape. The choice probe was presented either on the same location as the spatial WM memory cue (on-target condition) or other random locations (off-target condition). At the end of trial, participants answered whether the location of the test probe matched with the memory cue. The size of the area where stimuli were presented was also manipulated between the whole-field (A) and hemi-field (B) conditions. In the whole-field condition, all stimuli were presented in both visual fields and were limited to one of the visual fields in the hemi-field condition.

Results

The results showed no attention facilitation effect for the remembered location regardless of the distance between the memory cue and the choice probe. The mean response time was analyzed using a repeated analysis of variance (ANOVA) with the factors field size (whole -/ hemi -field conditions) and choice probe location (on-/off-target conditions). There was no main effect or interaction; field size: $F(1,26)= 0.49$, $p = .49$, $\eta_p^2 = .02$; choice probe location: $F(1,26) = 0.34$, $p = .56$, $\eta_p^2 = .01$; the interaction between them: $F(1,26)= .52$, $p =.48$, $\eta_p^2 = .02$. These results are shown in Figure 2-2.

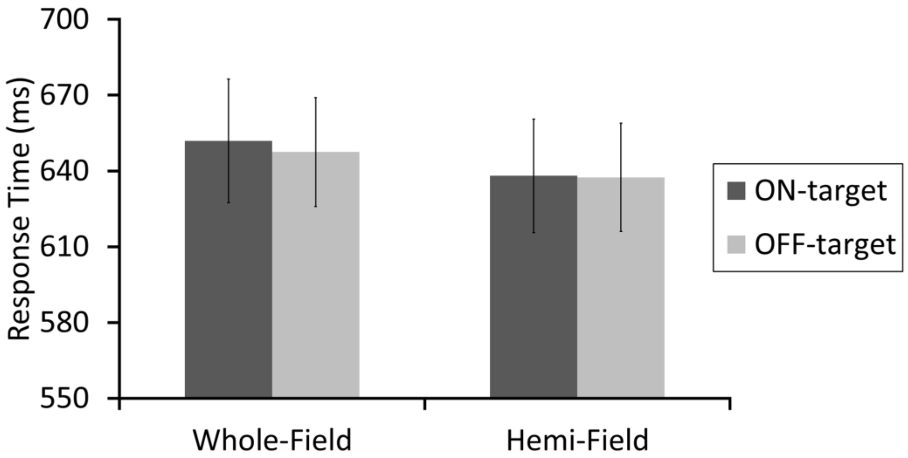

Figure 2-2. The result of Experiment 1. The left figure shows the mean response times of the choice probe task in the whole-field condition. The right figure shows the hemi-field condition. The dark and light gray bars correspond to the response times in the on- and off-target conditions, respectively. Error bars indicate standard errors.

Discussion

Experiment 1 showed no evidence for attentional facilitation during spatial WM maintenance. The response time for the choice probe was never faster in the on-target condition compared to the off-target condition. This result indicated that spatial attention neither focused on the remembered location nor was vaguely directed thereto, thus it seems to be consistent with the argument of Belopolsky and Theeuwes (2009). That is, spatial attention has no functional role in the rehearsal of spatial WM. It was, however, still possible that the behavioral index used in Experiment 1 simply did not have a sufficient power to uncover the target effect. This possibility was tested in Experiment 2.

Experiment 2

Experiment 2 had two purposes. The first one was to test whether spatial WM maintenance facilitates visual processing on the remembered location; that is, a reexamination of the results of Experiment 1 using ERP indices. The second goal was to examine whether spatial attention has a functional role in spatial WM maintenance. As in the previous ERP studies investigating this issue (Awh et al., 2000; Jha, 2002), the attention effect was measured as a possible increase of the P1/N1 amplitude evoked by the ERP probe. In addition, a difficult visual search task was inserted during the spatial WM retention interval before the ERP probe presentation, and the search array size was manipulated between 0, 6, and 8. It was expected that, if spatial attention has a functional role in spatial WM maintenance, (A1) the spatial WM performance should be impaired as the search array size increased, and moreover, (A2) the amount of attention deployed at the memorized locations, which were indexed by P1/N1, should not be changed regardless of the search demand, when the contents of WM were correctly retained. Finally, (A3) the attention effect should decrease when error trials in the spatial WM task were included in the ERP analysis, because a part of the errors should reflect the disruption of attention maintenance induced by the visual search. In contrast, if attention has no role in spatial WM maintenance, (B1) no impairment in the WM performance should be observed as the search array size increased, and (B2) the ERP attention effect should disappear when the visual search task was concurrently administered, because there should be no need to keep attention on the memorized locations when another attrition-demanding task was conducted.

Methods

Participants. Twenty-five volunteers (male: 17; female: 8; mean age: 23.28 years with SD 4.45 years) participated in the experiment. They provided informed consent before commencing the experiment and were compensated monetarily. The data of 7 participants were excluded because of excessive eye movements (see below for the criteria), thus 18 participants' data were analyzed.

Stimuli and Procedure. The task procedure is shown in Figure 2-3. All stimuli were presented on a gray screen of a 17 inch CRT monitor. E-prime 2.0 (Psychology Software Tools, Inc., Sharpsburg, PA, USA) was used to program the experiment. The viewing distance was about 60 cm. A fixation cross (0.7° × 0.7°) was continuously visible at the center of the screen throughout a trial. The sequence of events is illustrated in Figure 5.

Participants performed a dual task of a spatial WM and a visual search task. Each trial began with two spatial memory cues (black square, 0.5° × 0.5°) that appeared consecutively and indicated the to-be memorized locations. Each cue was presented for 100 ms, and was separated by a 100 ms blank. The purpose of the sequential presentation was to discourage participants from forming a shape-based representation connecting the two locations (Woodman & Luck, 2004; Study 1 of the current dissertation). Each memory cue was presented at a randomly selected location in the right or left rectangular region (width 2.9° × length 7.1°), with no appearance of two cues on the same side (e.g. when the first cue appeared in the left, the second was always in the right). The distance between the center of rectangle and fixation was 1.8°. The offset of the second memory cue was followed by a 500 ms blank, and then the visual search array was presented for 3,000 ms. Each search array was composed of 0, 6, or 8 items (black outlined square, 1° × 1°), each of which had a gap on one side. Search items appeared at random locations in 4 square regions (each 3.2° × 3.2°), and the distance between each item was at least 1.6°. Each of the 4 square regions was allocated at each 4 corners of the screen, and the center of each area was 7° apart from the central fixation. That is, these search areas were arranged such that they never overlapped with the memory cue region. The number of items in each square was limited to 2 in all 3 load size conditions. Namely, when the load size was 6, 3 square areas were randomly selected from the 4 regions, and 2 items were presented in each of the areas. When the load size was 8, 2 items appeared in each of all 4 regions.

Participants were required to perform a visual search task looking for two possible target shapes that contained a gap on either top or bottom side. One of the targets was always presented in the 6 and 8 load size conditions. Distractor items had a gap on either left or right side. Participants were asked to find the target and discriminate on which side the target item had a gap, by pressing keys on a standard keyboard (for half of participants, "j" indicated the top and "k" indicated the bottom side. For the remaining participants, "d" for the top and "f" for the bottom side). Speeded response was emphasized. It should be noted that no search item appeared in the load 0 condition and participants were not required to press any key.

The offset of the visual search array was followed by a 1,400 ms blank and then by test probes for the spatial WM task. Two test probes (black square, 0.5° × 0.5°, the same as the memory cues) were presented simultaneously for up to 2,000 ms. On 50% of all trials, the test cues were shown at the same place as the initial memory cues. On the remaining 50% of trials, one of the cues was presented at a new place which differed at least 1.9° from the original memory cue location. Participants had to make a response to discriminate whether one of the locations changed or not. Response accuracy was emphasized over speed. They responded in the spatial WM task by pressing a key on the keyboard (for the participants who used the "j" and "k" keys in the search task, "d" or "f" keys were used in the spatial WM task, with "d" indicating location change, and "f" indicating no change. For the remaining participants who used "j" and "k" keys in the spatial WM task, "j" indicated location change and "k" indicted no change). Each trial was followed by a 900-1000 ms inter-trial interval (ITI).

In two thirds of all trials, an ERP probe (white dot, 0.5° × 0.5°) was presented for 100 ms during the blank period between the visual search and the test probe onset. The interval between the offset of the visual search array and the onset of the ERP probe was randomly taken from the time range between 700 and 800 ms. Participants were instructed to ignore the ERP probe. In the rest of trials, the ERP probe never appeared (the no-probe condition). There were 2 conditions regarding the probe location. In the on-target condition, an ERP probe was presented at the same location as one of the memory cues. In the off-target condition, the ERP probe appeared in either of the two rectangular regions, but its location was at least 1.9° apart from the memorized positions. The ratio of on- to off-target condition was 1:1.

Each of 90 blocks consisted of 12 trials. At the end of each block, accuracy rates for the spatial WM and the visual search task were displayed on the screen. The experiment was divided into 2 sessions which were conducted on different days. All conditions were randomized in a trial-by-trial manner.

Electroencephalogram Recording and Analysis

Data Acquisition. Electroencephalogram (EEG) was recorded with a sampling rate of 500 Hz using a band-pass filter of 0.05 - 100 Hz (AC recording) by the Neuroscan SynAmp2 System (Neuroscan Inc., Charlotte, NC, USA) and EasyCap electrodes (EasyCap GmbH, Herrsching, Germany). Data were obtained from 20 electrodes (Fz, F3, F4, Cz, C3, C4, Pz, P3, P4, PO3, PO4, P7, P8, PO7, PO8, POz, O1, O2 and two ear lobes). All electrode impedances were kept below 10 kΩ. The VEOG and HEOG were also recorded in order to exclude possible ocular artifacts. The positions of EOG electrodes were the same as Experiment 1. All electrodes except EOGs were referenced to an electrode on the tip of nose during recording, and re-referenced offline to the algebraic average of the two ear lobes. A bipolar derivation was used for EOGs.

Artifact Rejection. In order to remove trials containing ocular artifacts, the following two-step procedure for epoching and artifact rejection was applied. First, trials with possible eye movements during the entire retention interval were excluded from the analysis. In these trials, retinotopical topography could be largely altered between the period of spatial WM encoding and of the ERP probe presentation, and therefore the ERP attention effect calculated as the difference between the on- and off-target conditions could be invalidated. For this purpose, EEG data were epoched from -100 before to 5100 ms after the memory cue onset. The end of these epochs corresponded to 400-500 ms after the ERP probe onset. A 100 ms interval prior to the memory cue was used as baseline. Since the epoched time range was relatively long (5,200 ms), slow voltage changes, which were not necessarily related to an actual eye blink or eye movement were possibly counted as artifacts. In order to avoid this problem, a max-min algorithm was applied. The whole epoched range was separated into 75 ms bins and trials in which the difference between the maximum and the minimum VEOG amplitudes exceeded 75 μV in one of the bins were discarded. The same method was applied for the HEOG data but with an exclusion criterion of 30 μV, instead of 75 μV, which ensures that eye movement is always less than 2° (See Method section of Experiment 1 for details). Consequently, data of 7 participants with rejection rates over 30% were excluded from analysis. Trials with erroneous response in the visual search task were also rejected. After this exclusion procedure, epochs that corresponded to the ERP probe processing were extracted as the second step of the analysis. The time ranges from -100 before to 400 ms after the ERP probe onset was epoched. Amplitudes were once again corrected to the 100 ms interval before the ERP probe onset as baseline. Finally, these segmented data were averaged separately for each condition to obtain ERP waveforms. Two different types of averaging were conducted. In the first one, trials with incorrect responses in the spatial WM task were excluded from the analysis. In the second one, all trials were included.

Quantification of the Probe-Evoked ERP. Firstly, the data of the no-probe condition was subtracted from those in the condition where the ERP probe appeared in order to erase the after-effect of the memory cue and visual search processing on the ERP waveforms. Next, since both the P1 and N1 amplitudes showed their maximum at the PO7/8 electrode site contralateral to the visual field where the ERP probe was presented (Figure 2-5A), ERP waveforms recorded at these sites were calculated and submitted to statistical analyses. The amplitudes of P1 and N1 were quantified as the mean amplitudes in the 80-120 ms and 140-180 ms time period after the ERP probe onset, respectively.

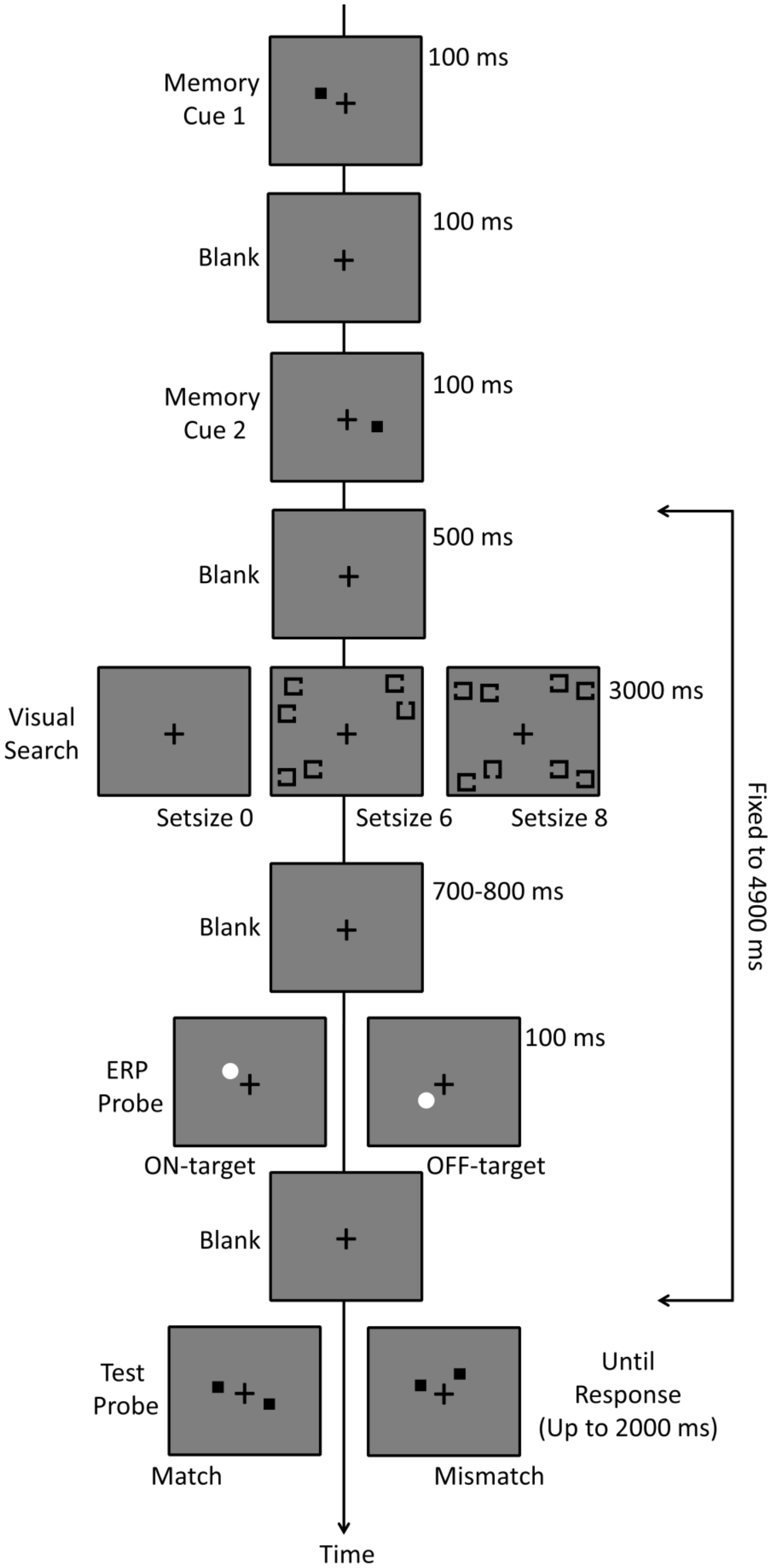
Memory
Cue 1
100 ms
Blank
100 ms
Memory
Cue 2
100 ms
Blank
500 ms
Visual
Search
3000 ms
Setsize 0
Setsize 6
Setsize 8
Blank
700-800 ms
ERP
Probe
100 ms
ON-target
OFF-target
Blank
Fixed to 4900 ms
Test
Probe
Until
Response
(Up to 2000 ms)
Match
Mismatch
Time

Figure 2-3. Schematic diagrams of the experimental procedure in Experiment 2. A trial consisted of spatial WM memory cues, the first blank, a visual search task, the second blank, a ERP probe, the third blank, and spatial WM test probes. At the encoding phase, two memory cues were presented sequentially separated by a 100 ms blank. Cues were always presented in different visual fields. The visual search task had 3 load conditions (0, 6, and 8). In the load 0 condition, search stimuli never appeared on the screen. In the load 6 and 8 conditions, search items appeared in the peripheral areas of the screen. Targets had a gap on the top or bottom side, and distractors had a gap on the left or right side. One of the items was always the target, and participants were required to identify which side of the target had the gap. The ERP probe (white dot) was presented in 2/3 of the trials. The ERP probe was presented at the locations either where the to-be-memorized cues appeared (the on-target condition) or other random places (the off-target condition). At the end of trial, two test cues were presented simultaneously, and participant had to answer whether their locations matched the remembered locations. Throughout a trial, participants were strictly instructed to fixate on the central cross.

Statistical Analyses. P1 and N1 data were separately analyzed by a repeated-measures ANOVA with the factors probe location (on-/off-target) and search array size (0, 6, and 8). Accuracy rates for the spatial WM task were also compared across conditions using repeated-measures ANOVAs with the same factors as the ERP analyses. Response time data for the visual search task was examined by a *t*-test between the load 6 and 8 conditions. When appropriate, the Greenhouse-Geisser correction was applied for nonsphericity, and Bonferroni correction for post-hoc pairwise comparison.

Results

Behavioral data

The behavioral data showed a clear interference from the visual search task on the spatial WM performance, as shown in Figure 2-4A. The main effect of search load was significant, $F(1.42, 24.08) = 41.50$, $p < .001$, $\eta_p^2 = .71$. Post hoc pairwise comparisons showed that the accuracy in the load 0 condition (i.e. no visual search) was higher (91.50%) than both in the load 6 (84.56%, $p < .001$) and load 8 conditions (84.68%, $p < .001$). There was, however, no significant difference between the load 6 and 8 conditions ($p > .99$). Moreover, the response time in the load 8 condition of the visual search task was significantly slower (954.58 ms) than in the load 6 condition (1002.39 ms), $t(17) = -6.20$, $p < .001$, Cohen's $d = -1.46$, indicating a serial attention deployment during the search. The response time data is shown in Figure 2-4B.

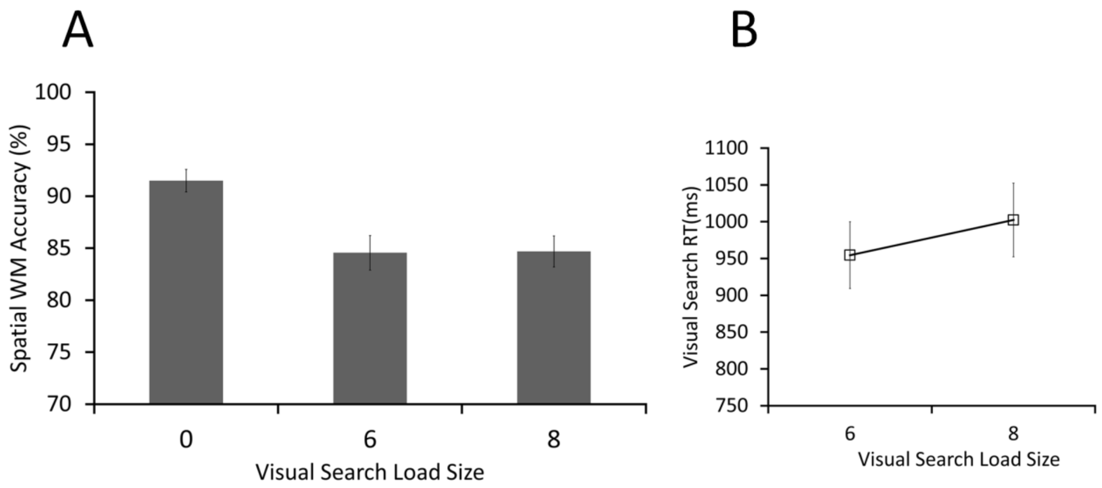

Figure 2-4. Behavioral results in Experiment 2. (A) Spatial WM accuracy (%) in each search load conditions and (B) the mean response times (ms) in the load 6 and 8 conditions of the visual search task. Error bars indicate standard error.

ERP Data

Analysis with Correct Trials of the Spatial WM Task. When only the correct trials of the spatial WM task were used to calculate the probe-evoked ERP waveforms, a clear attention facilitation effect was observed in the N1 amplitude. In addition, and most critically, this facilitation effect remained unchanged even when the concurrent visual search was conducted. The N1 amplitude showed a main effect of probe location, $F(1, 17)= 5.46$, $p = .03$, $\eta_p^2 =.24$. but not of search load size, $F(2, 34)= 1.50$, $p = .24$, $\eta_p^2 =.08$. Importantly, the interaction between the probe location and load size also did not reach significance; $F(1.42, 24.11)= .09$, $p = .91$, $\eta_p^2 =.006$, indicating that the concurrent visual search performance did not affect the N1 attention effect. The on-target N1 amplitude was consistently larger (-2.03 μV) than the offf-target (-1.61 μV) regardless of the visual search load size (see Figure 2-5D). On the other hand, the P1 amplitude showed no significant main effect or interaction; probe location: $F(1, 17)= .12$, $p = .73$, $\eta_p^2 =.007$; load size: $F(2, 34)= .76$, $p = .47$, $\eta_p^2 = .04$; interaction between them: $F(1.44, 25.44)= .50$, $p = .56$, $\eta_p^2 = .03$. The ERP waveforms are shown in Figures 2-5B and D.

Analysis with All Trials. When both error and correct trials of the spatial WM task were included to the analysis, no evidence of attention disruption caused by the concurrent visual search task was found. Given that the spatial WM performance was impaired in the load 6 and 8 conditions, this result was rather surprising. The N1 amplitude only showed a main effect of probe location; $F(1, 17)= 5.13$, $p = .04$, $\eta_p^2 = .23$, but not of search load size or the interaction between them; load size: $F(2, 34)= 1.59$, $p = .22$, $\eta_p^2 = .09$; their interaction: $F(1.48, 25.15)= 0.09$, $p = .85$, $\eta_p^2 = .05$. The N1 amplitude in the on-target condition was consistently larger (-3.90 μV) than the off-target condition (-3.22μV), regardless of the visual search load size. Finally, the P1 amplitude did not show any significant main effect or interaction; probe location: $F(1, 17)= 0.04$, $p = .85$, $\eta_p^2 =.002$; load size: $F(2, 34)= 0.83$, $p = .44$, $\eta_p^2 = .05$; interaction between them: $F(2, 34)= 3.14$, $p = .06$, $\eta_p^2 =.16$. The ERP waveforms are shown in Figure 2-5C and D.

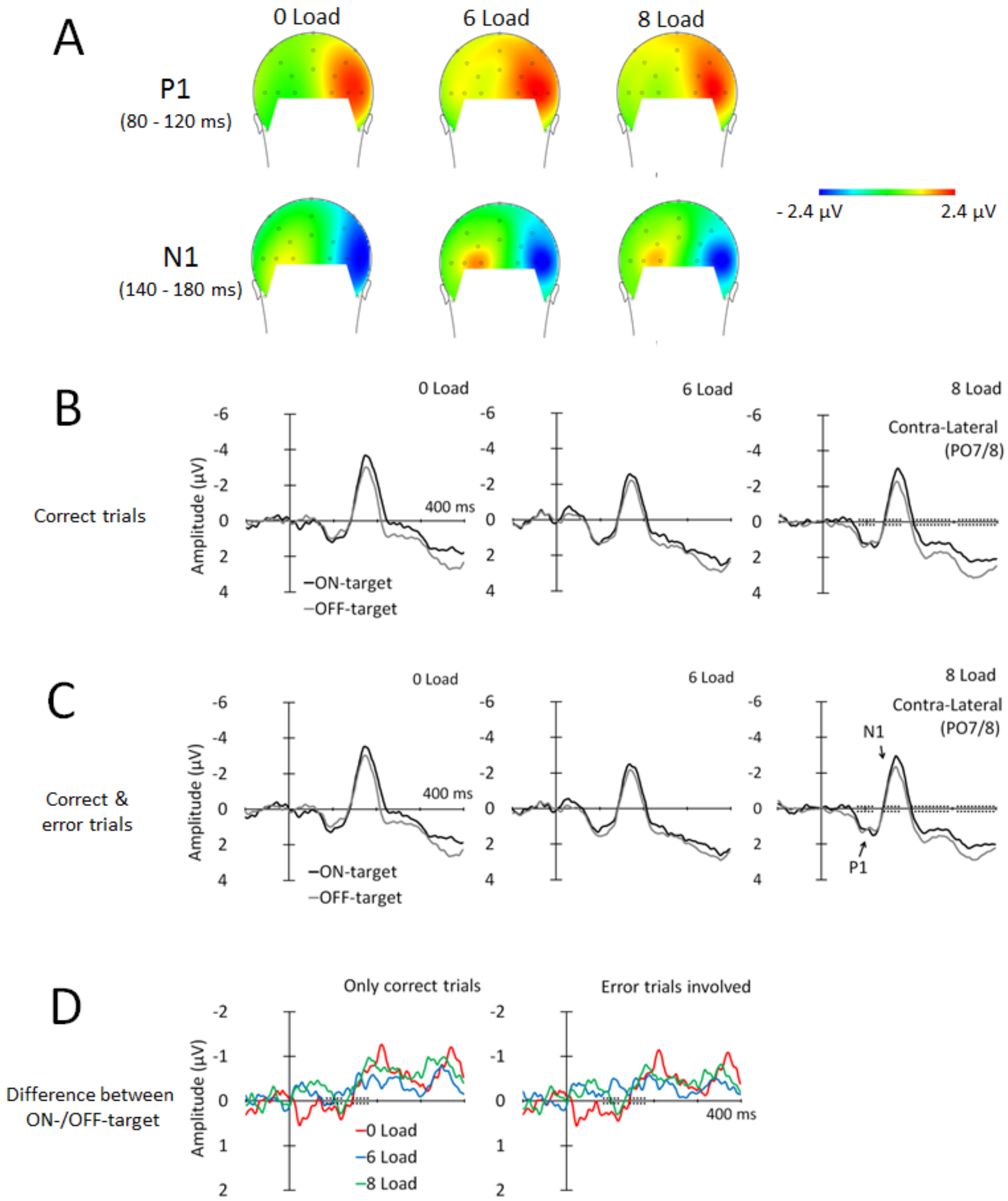

Figure 2-5. ERP results in Experiment 2. (A) Interpolated voltage topographical maps for P1 (80-120 ms) and N1 (140-180 ms) in the load 0, 6, 8 conditions, when the ERP probe was presented in the left visual field. Note that the amplitudes were maximized at the contralateral tempro-occipital sites (PO7/8) in all load conditions. (B) ERP waveforms locked to the ERP probe onset in the load 0, 6, 8 conditions, when only correct trials of spatial WM task were averaged. Black lines correspond to the on-target, and gray lines to the off-target condition. The dotted lines on the x-axis of the rightmost figure indicate the time windows used in the analyses, corresponding to the P1, N1, 200-300 ms, and 300-400 ms time ranges. (C) ERP waveforms calculated from all trials including errors of the spatial WM task. (D) Difference waveforms obtained by subtracting the off-target from the on-target condition. Red, blue, and green lines correspond to the load 0, 6, and 8 conditions, respectively. The left figure shows the wave calculated only from correct trials of the spatial WM task, and the right from all trials including errors in the spatial WM task.

Discussion

Experiment 2 provided rather conflicting results. As summarized below, the data might suggest that spatial attention was actively maintained at the to-be-memorized locations, although its functional significance was not proven.

First, the N1 amplitude was clearly enlarged when the probe appeared on the remembered location as compared to other random positions, indicating that spatial attention was kept focusing on the memorized location during the maintenance period. In other words, the current experiment successfully replicated the findings of the previous ERP studies on this issue (i.e. Awh et al., 2000; Jha, 2002). An alternative explanation of this result might be that it was produced by the successive presentations of two stimuli (i.e. the memory cue and the ERP probe) on the same location. This interpretation, however, is quite unlikely because it is well known that when two stimuli are presented successively with a long interval (more than 300 ms) and they are only passively observed, the P1 and/or N1 amplitudes evoked by the second stimulus are reduced as compared to when the second stimulus appeared alone (Prime & Ward, 2004; 2006), an observation that has been interpreted as evidence of inhibition of return. In contrast, when participants actively attended at the location where the first stimulus is presented, the P1 and/or N1 amplitudes elicited by the second stimulus become larger, indicating an attentional facilitation of the second stimulus processing (Mangunet al., 1993). Therefore, it is not probable that the enlarged N1 amplitude observed in the current experiment was induced by the successive presentation of stimuli.

Second, the N1 attention effect measured as the difference between the on- and off-target conditions remained constant regardless of the attentional demand posed by the visual search task. Importantly, the visual search task robustly interfered with the WM task as evidenced by the WM performance impairment between the load 0 and 6, or the 0 and 8 conditions. Therefore, the insensitivity of the N1 attention effect to the additional cognitive demand might suggest that spatial attention was *actively* maintained at the to-be-memorized locations and was protected from the interference caused by visual search. Although these first and second results seem to support the functional significance of spatial attention in WM maintenance, the rest of the data argued against it.

In particular, the third finding of the current study casts a doubt on the functional significance of spatial attention in spatial WM maintenance. Although the visual search task interfered with the spatial WM performance, the magnitude of the impairment was not sensitive to the increase of search array size from 6 to 8. Note that the WM deficit caused by the mere execution of the dual task, which was detected as the performance difference between the load 0 and 6, or 0 and 8 conditions, could be due to an increase of a general cognitive demand, which is not specifically related to WM maintenance. Therefore, whether the WM performance was affected by the change of the array size between 6 and 8 was the most critical test to judge the functional significance of spatial attention. Thus, the current data seem to indicate that spatial attention has no causal effect on spatial WM maintenance.

The fourth finding was also inconsistent with the prediction derived from the attention-based rehearsal hypothesis. As noted before, the N1 attention effect was robustly observed regardless of the visual search demand, indicating the active maintenance of spatial attention during WM maintenance. Surprisingly, the same pattern of results was also observed when the error trials of the spatial WM task were included in the analysis. These results suggest that the impairment in the accuracy data caused by visual search was not accompanied by the loss of active attention maintenance.

Altogether, Experiment 2 suggests that, although spatial attention was actively maintained at the to-be-memorized positions, its functional significance still needs further examinations. Before proceeding to the conclusion that spatial attention plays no critical role in spatial WM maintenance, an alternative interpretation has to be considered. That is, the visual search task might have failed to effectively deprive attention resource from the concurrent spatial WM task. It should be emphasized that the interpretations of the abovementioned third and fourth findings were strongly depending on the assumption that the increase of the visual search items should demand more attentional resource to perform it, and therefore it should disrupt the spatial attention used for the maintenance of spatial WM more severely. It is worth noticing that since the response time of visual search was slower in the load 8 than in 6 condition, it was highly plausible that attention was serially deployed on each search items. However, the presence of serial search does not guarantee that it actually deprive the attention from the concurrent task. In fact, there are some reasons to support this alternative interpretation, which will be further discussed in General Discussion of Study 2.

General Discussion of Study 2

The current study aimed to verify the attention-based rehearsal theory of spatial WM, by re-examining two lines of evidence supporting this theory. The first one was the attentional facilitation effect during spatial WM maintenance, which indicates whether spatial attention was allocated on the to-be-memorized locations during spatial WM maintenance (Awh et al., 1998: Awh et al., 2000: Jha, 2002). The second one was the attentional deprivation effect on spatial WM performance, which suggests whether spatial attention plays a functional role in spatial WM maintenance (Awh et al. 1998; Oh & Kim, 2004; Woodman & Luck, 2004). Although these effects have been confirmed in several studies, others reported counter-evidence for both findings (Belopolsky & Theeuwes, 2009; Chan et al. 2009). In addition, a methodological concern was found in an ERP study that reported the attentional facilitation effect (Awh et al., 2000). Therefore, the current study re-examined these effects, using similar methods as previous studies, but avoiding possible confounding factors.

The attentional facilitation effect was tested in Experiment 1 using behavioral indices, and Experiment 2 measuring attention-related ERP components. Experiment 1 failed to find the target effect, whereas Experiment 2 successfully confirmed it. The reason of the discrepancy between two experiments is unclear. Given the validity of the behavioral method established in the attention literature (e.g. Posner & Cohen, 1984), it might be the case that the target effect size was so small that the statistical power of the behavioral measures in Experiment 1 was too weak to detect it, possibly due to the noise in the item identification and response selection processes. This possibility might be applied to the discrepancy between Awh et al. (1998) and Belopolsky and Theeuwes (2009) too, because they also used the same behavioral index. In contrast, the ERP indices are thought to more directly reflect cognitive processing of stimulus without further complications. Thus, the ERP indices and the results of Experiment 2 are more reliable than those of Experiment 1. This result suggests that spatial attention might be continuously allocated on the to-be-memorized locations during spatial WM maintenance.

In addition, Experiment 2 examined the functional role of attention in spatial WM maintenance. To this aim, a visual search task was interpolated during the retention interval of spatial WM, and the effect of attention deprivation on spatial WM maintenance and the spatial attention allocation on the to-be-memorized locations was examined. Data showed mixed results. First, it was found that the attention strength on N1 was unchanged regardless of the size of visual search demand, suggesting an active maintenance of spatial attention. However, behavioral data showed that the increase of search items from 6 to 8 did not affect the performance of the spatial WM task. Moreover, the size of the N1 attention effect did not change even when the error trials of the spatial WM task were included in the analysis. These latter two findings reject the simple interpretation that spatial attention plays a critical role in the maintenance of spatial WM.

How can these results be integrated to give a logically consistent interpretation? As already noted in the Discussion section of Experiment 2, the findings that contradicted with the predictions from the rehearsal hypothesis suggests either that spatial attention is totally irrelevant to spatial WM maintenance, or that visual search might have failed to effectively deprive attention from the spatial WM maintenance. The first possibility seems difficult to reconcile with the active maintenance of spatial attention, given that attention resource is fundamentally limited and therefore should be effectively allocated to the cognitive processes that are relevant at the time. On the other hand, there are two possible theories that explain the co-existence of the successful visual search performance, that is, the failure of attention deprivation, and the active maintenance of attention during WM retention. The first one is the hierarchical structure theory of WM, the second one is the divided attention hypothesis.

Hierarchical Models of WM

Recent studies proposed a hierarchical model of WM, which assumed that the items in WM are not always maintained in an equal status but in different statuses in a hierarchical structure. For instance, Cowan (1988) proposed two levels of hierarchy; activated long-term memory (aLTM) and focus of attention. aLTM stored information that was recently activated but irrelevant for the ongoing task (e.g. the contents of a TV program watched 5 minutes ago). aLTM system does not have a limited capacity, and therefore we can store as much information as we want inside it, but the contents could fade out passively as time passes. Attention has to be focused on the aLTM contents (i.e. focus of attention) in order to make the memory contents accessible by ongoing cognitive processes and to prevent them from the passive decay. This focus of attention has a limited capacity of 4 ± 1 items (Cowan, 2001).

This and other models proposed in studies such as those of Oberauer (2002) and Unsworth and Engel (2007) share the concept that WM is composed by hierarchical layers, and that the highest layer needs focus of attention to retain the memory contents. Recent studies utilizing the multi-voxel pattern analysis of functional imaging and EEG data have supported this hypothesis by showing that only the contents in focus of attention could be decoded from the neural activity (Lewis-Peacock & Postle, 2012; LaRocque, Lewis-Peacock, Drysdale, Oberauer, & Postle, 2013).

If these hierarchical structure models could be applied to spatial WM too, it could explain the conflicting results of the current study. A possible account could be as follows. Firstly, the memory cues were stored and maintained in the highest layer of the structure, such as focus of attention. Then, when the visual search task was administrated and the location memory became relatively unimportant temporarily, the location information was sent to the other layer such as aLTM. After visual search was completed, the location memory was sent back to the highest layer again, to prepare for the test phase of the spatial WM task. If this was the case, it is not surprising to find that the attention effect seemed to be insensitive to the insertion of the visual search task, especially because the ERP probe was presented after the completion of the visual search task.

Divided Attention

An alternative possibility for accounting the complex results of the current study is divided attention. It has been proposed that we have an ability to split attention into approximately four different positions simultaneously (Sears & Pylyshyn, 2000; Eimer & Grubert, 2014). In Experiment 2, participants were asked to retain only two locations, thus the other two attentional spots might have been available for the visual search task.

Since it is not possible to distinguish these possibilities based only on the data from the current study, future research is necessarily required. One of the possible methods to clarify the issue is presenting the ERP probe when participants are actually performing the visual search task. If the attention effect was still confirmed in this setting, it will suggest that the location information is stored in the highest layer, and thus it would support the divided attention account. On the other hand, if the effect was not observed, it would support the hierarchical structure account.

The Lasting Effect of Probe-Induced Attention

The another concern found in Experiment 2 was that the attention effect between the on- and off-target conditions was observed only in the N1, but not P1 time range. In addition, ERP waveforms in Experiment 2 implied that this effect remained long after the N1 period and lasted until the end of the 400 ms epoched range (see Figures 2-5B and C). I conducted an additional analysis to confirm this lasting effect. The entire time period after post-probe 200 ms was separated into two ranges (200-300 ms/ 300-400 ms in respect to the ERP probe onset), and applied a repeated-measure ANOVA with the factors of probe location and search load size. The significance alpha level was set to .025 in order to avoid the type I error of multiple comparison. The results showed that the attention effect was significant through the two time ranges. In addition, visual search insertion did not affect the effect. This trend was not affected by the inclusion of error trials. The averaged amplitudes in both the 200-300 ms and 300-400 ms range showed a significant main effect of probe location, when only correct trials were used; $F(1, 17)=12.74$, $p = .002$, $\eta_p^2 = .43$ for 200-300 ms and $F(1, 17) = 11.87$, $p = .003$, $\eta_p^2 = .41$ for 300-400 ms, and when error trials were involved; $F(1, 17) = 11.385$, $p = .004$, $\eta_p^2 = .40$ for 200-300 ms, and $F(1, 17) = 8.585$, $p = .009$, $\eta_p^2 = .34$, for 300-400 ms, respectively. Nevertheless, the interaction between probe location and search load size was not significant for both cases ($p > .1$). These results indicated that the attention effect sustained for at least 200 ms after the N1 time period. Although it is difficult to identify the nature of this late effect after N1, it probably reflects a modulation induced by spatial attention on the memorized locations. Because first, it is the difference between the probe location conditions, and second, previous studies have shown that attention modulations can be observed within this time range too (Anllo-Vento, Luck, & Hillyard, 1998). Thus, the attentional facilitation was relatively long-lasting, possibly reflecting top-down re-entrant modulations (Zhang & Luck, 2009).

If this interpretation is correct, where was the spatial information in WM stored? The top-down re-entrant modulation means that location information was retained in other regions but not in visual cortex itself, and ERP probe onset triggered top-down signal (i.e. attention) from the area to visual cortex. One possible candidate for this region is aLTM in WM hierarchical layers. Recent studies, however, assume that the neural substrate of aLTM is the temporal strength change of synaptic connection at sensory cortex (Mongillo, Barak & Tsodyks, 2008; Erickson, Maramara & Lisman, 2010; Nee & Jonides, 2013; D'Esposito & Postle, 2014). Therefore, if spatial WM information is in aLTM, it should be also stored at visual cortex. This interpretation of the results is possible if the delay of ERP modulation reflects memory transition from aLTM to focus of attention. However, this interpretation is inconsistent with the top-down re-entrant explanation. Another candidate substrate for the store of spatial information is the superior colliculus. It has been argued that superior colliculus has an important role in spatial attention function (Ignashchenkova, Dicke, Haarmeier & Their, 2004; Katyal, Zughni, Greene & Ress, 2010), and that this area equips topographic map of space (Marino, Rodgers, Levy & Munoz, 2008; Katyal et al., 2010). Moreover, superior colliculus is anatomically separated from visual cortex.

Thus if spatial WM information was retained here, the delayed ERP enhancement can be understood in the context of top-down re-entrant modulation. Further research is warranted to clarify the implication of this finding.

Limitation of the current study and next steps

I should note here the limitation of the ERP probe method that was employed in this study. This procedure has been commonly used by previous studies examining the attention-based hypothesis (Awh et al., 2001; Jha, 2002). According to these studies N1 enhancement effect in the current result could prove active maintenance of spatial attention. This technique, however, has an essential concern in that ERP probe measures attentional effect only at one time point (i.e. when ERP probe appeared). Therefore, strictly speaking, the current results show that spatial attention focused on the remembered place when ERP probe appeared, but cannot show that it was maintained thorough the retention interval. If we assume that spatial information was stored in different system from spatial attention (e.g. aLTM), and that participants expected ERP probe appearance and directed attention to the remembered place with the help of the memory right before onset of the probe, then the ERP probe method could detect the spatial attention effect. How can we avoid this problem when examining whether spatial attention persists during WM retention interval, and whether it has a functional role for its process, avoiding this problem?

A possible method to assess the significance of attention is to test whether spatial attention effect remains or not during interval between trials. In the current procedure, this could be achieved by presenting ERP probe during trial intervals. If the attentional effect disappears after the end of the trial, it would suggest that attention has some role in the WM maintenance process. On the other hand, if attention effect persists during the trial interval, this result would indicate that attention has no functional significance and that it is just a passive effect. Although, this technique has the same problem as the method used in the current study 2 - that is, the method can examine the attention effect only at one time point - the results obtained by using this method could yield suggestive evidence.

The other but more direct solution is time frequency analysis of EEG data. Recent studies using this method has revealed that attention induces gamma- and alpha-band oscillation at contra- and ipsi-lateral site to attended visual field, respectively (Gruber, Matthias, Muller, Keil & Elbert, 1999; Worden, Foxe, Wang, Simpson, 2000; Bollimunta, Mo, Schroeder, & Ding, 2011). It has been said that gamma wave has important role for attention (Rouhinen, Panula, Palva & Palva, 2013) and alpha wave reflects inhibition of task irrelevant information (Klimesch, Sauseng & Hanslmayr, 2007). In addition, these synchronized activities have been also observed during WM maintenance process (vanDijk et al., 2010; Roux & Ulhaas, 2014). Analyzing the power fluctuation of each frequency in current EEG data might be informative, because it will make me able to access neural activities relating WM maintenance process, thorough the whole retention interval. Especially, examining the power change of these oscillations around the visual search insertion will offer numerous suggestions about functional role of attention in WM maintenance. This analysis has to be performed in future research.

To conclude, the current results might suggest that spatial attention is allocated on the memorized locations during the spatial WM retention interval, and this attention is maintained not passively but actively, protecting it from the demand from the other concurrent task. Note that I just obtained indirect evidence for the functional significance of spatial attention, and for its persistence though the WM retention interval. Thus further research is needed to clarify these problems. However, the findings in the current study were consistent with the attention-based rehearsal theory of spatial WM (Awh et al.,1998; Awh & Jonides, 2001).

General Discussion

The current dissertation examined two problems that are theoretically relevant for the understanding of the fundamental structure of the visuo-spatial WM mechanism; namely, the separation between visual and spatial WM systems and the role of attention in WM maintenance. These two topics are closely related to each other. Since it has been hypothesized that different sub-categories of attention (e.g. Scolari et al., 2014) might support corresponding different types of WM (Barnes et al., 2001), it is possible the limitation of WM capacity in each region is caused by that of attention. Evidence supporting this proposal, however, has been scarce and sometimes contradicting.

As for the first issue, Wood (2011) recently reported interference between shape and spatial WM capacities. Since this finding could undermine the fundamental assumption of the visuo-spatial WM separation hypothesis (Logie, 1995), a detailed investigation was required. Study1 examined this problem using a dual task paradigm. First, I replicated the relevant experiment in Wood (2011) with strict controls on the several methodological concerns found in in the original study. The data failed to show the expected result in all three experiments (Exp. 1, 2, and 3). I suspected, however, that these negative results might have resulted simply from the fact that the size of the target effect was small and therefore the sample size in each experiment was not sufficient to detect it. Thus I conducted another replication of the original experiment with an unusual big sample size (N = 90; Exp. 4), and succeeded to reproduce the significant interference. The estimated effect size, however, remained very small (Cohen's d = 0.24). Thus, these results strongly suggested that shape and spatial WM capacities are mostly independent, and supported the visuo-spatial WM separation (Logie, 1995).

The second topic of the dissertation was the role of attention in WM maintenance. Different theoretical accounts have been proposed on this topic, and no consensus has been achieved so far (Awh et al, 1998; Luck & Vogel, 1997; Wheeler & Treisman, 2002). Specifically, even the long-standing assumption of the critical role of spatial attention in spatial WM maintenance (Awh et al., 1998; Awh & Jonides, 2001) has been questioned recently (Belopolsky & Theeuwes, 2009; Chan et al., 2009). Thus, I tackled this problem in Study 2.

The attention-based rehearsal theory of spatial WM predicts that spatial attention should be continuously focused on the remembered location during the retention interval (Awh et al., 1998; Awh & Jonides, 2009). Experiment 1 examined this prediction using a behavioral index of spatial attention, and failed to find the effect. Nevertheless, since this negative result could simply be due to the insensitivity of the measurement, Experiment 2 tested the same problem again using ERP (P1/N1) indices of spatial attention. A point of concern is that to observe the effect of spatial attention is not sufficient to prove its functional significance, because spatial attention could remain at the remembered locations as a passive after-effect of the encoding process. Thus, I inserted a visual search task during the WM retention interval, and assessed how the manipulation of the search load size affected the WM performance and the allocation of spatial attention. Results showed a clear effect of attention at the remembered positions as compared to other spatial locations. In addition, the amount of attention was unchanged regardless of the search load size. These results might suggest that the spatial attention is not just a passive after-effect, but actively maintained during the WM retention interval. On the other hand, some inconsistencies with the theoretical predictions were also found, which suggested that the attention deprivation by visual search might have been insufficient in the current setting. To summarize, although the functional significance of attention was not completely confirmed, Study 2 might suggested an active and strong sustention of spatial attention in spatial WM maintenance, and current results were consistent with the attention-based rehearsal theory (Awh et al., 1998; Awh & Jonides, 2001).

Relationship between Object and Spatial WM

Given that Study 1 confirmed that feature and spatial WMs have mostly separated capacities, the next important question will be whether the WM for integrated objects shares the same storage resource with spatial WM. The clarification of this issue is of a huge theoretical importance, since if object and spatial WM do not share the common resource, it will provide strong counterevidence for Wheeler and Treisman (2002) hypothesis, which argued that spatial attention is necessary for maintaining integrated objects. Although Wood (2011) already reported interference between these two domains, two methodological concerns were found in his study. First, the effect size of the reported interference might have been small and thus functionally insignificant, as Study 1 in the current thesis has revealed for the shape-spatial interference. Second, since the task order was fixed in Wood (2011) (i.e. spatial then object), the object encoding always occurred during the maintenance of spatial WM, and therefore the interference could be caused by the *encoding*, but not the *maintenance* process of object WM. Thus, new experiments with strict controls on these factors are strongly required.

In addition, this issue can also be evaluated by a more direct examination of spatial attention, especially its persistence and functional significance during object WM maintenance, as Study 2 in the current dissertation examined for spatial WM.

Relationship between Other Sub-Domains of Visual WM

The next concern for the future investigation is whether other sub-domains of visual WM share the same storage resource. Woodman et al. (unpublished data in Zhang et al. 2012) has already shown that strong interference was observed when color and orientation WM tasks were concurrently administered, suggesting that different subdomains of visual WM could share a limited unitary resource. Nevertheless, the capacity sharing in other sub-domains of visual information (e.g. shape, face, and house) have not been examined so far. A systematic investigation of the WM interference across visual WM subdomains is required in future research, using the same dual task paradigm employed in Study 1 in the current thesis. Such investigations might shed a light on whether WM capacity is dissociated not only between visual and spatial categories, but also among subdomains of visual information.

In addition, if such independences are truly confirmed, it will evoke the discussion about the overlap between the attention and WM systems again. Suggesting evidence for this domain-specific overlap between attention and WM has been already accumulated. For example, using the fMRI technique, D'Esposito and his group showed that WM maintenance for face and house induced continuous activities in the visual area specialized for each information processing (i.e. the fusiform gyrus and parahippocampal area for face and house, respectively; Ranganath, Cohen, Dam, & D'Esposito, 2004), which closely resembled the effects caused by attention directed at each specific category (O'Craven, Downing, & Kanwisher, 1999). Therefore, it is quite possible that domain specific attention supports the maintenance of corresponding WM system. Similarly, Sreenivasan et al. examined the same problem in the face category (Sreenivasan, Katz, & Jha, 2007). Irrelevant probe (grayscale noise) was presented during the face WM retention interval, and ERP components corresponding to face processing (i.e. N170; Bentin, Allison, Puce, Perez, & McCarthy, 1996) were examined. The results showed that the irrelevant probe elicited a N170-like ERP waveform. Thus, the fact that a N170-like response was observed even though the probe was completely different from face possibly suggested that the face-related attention was retained during face WM maintenance, and modulated the cortical processing even towards probes quite dissimilar to face. However, to test whether attention is directed to the remembered information is not sufficient to prove its functional significance, as I have argued throughout the current thesis. Whether a deprivation of domain specific attention disturbs the corresponding WM maintenance should be examined in future studies too.

The current dissertation provided new data to clarify the important, but unsettled issues in the research on visuo-spatial WM. These basic data are necessary to constitute the foundation for the further theoretical development in this research area. Since WM has been thought as the most primary function sustaining our mental life (Baddeley, 2003; 2010), a large number of studies have investigated its mechanisms, and a flood of findings has been produced so far. Nevertheless, many theoretical assumptions and arguments still remain controversial, and even seemingly well-accepted findings could sometimes be questioned by new data. In order to obtain a comprehensive understanding on this issue, it is necessary to conduct more systematic, detailed, and through examinations on various aspects of this cognitive function, and I believe that the current dissertation provided an example of such endeavor. Reliable scientific knowledge can be unveiled, only when these small, but strict steps are accumulated.

The format of WM representation

The Final open question is what space our brain represents WM contents in. Since attentional modulation is executed at sensory cortex (Kastner & Ungerleider, 2000), information in focus of attention might be organized at the same space as perception (e.g. spatial information represented in topographic space of visual cortex). Thus, if attention is a unique mechanism for WM maintenance, WM contents might be also expressed in this space. However, recent studies have revealed that there is different WM storage system than attention (i.e. aLTM). Given that WM contents can be retained by aLTM, how are they represented?

According to recent studies, contents in aLTM might be represented in the same space as attention and perception. As I noticed above, it has been supposed that the neural mechanism of aLTM is temporal strength change of synaptic connection at sensory cortex. In this case, spatial memory in aLTM might be represented in topographic map of visual cortex. Moreover, if this hierarchical WM structure can be applied to other WM systems, color memory in aLTM might be stored in feature space of visual cortex, and phonological memory in aLTM might be retained in phonological map of auditory cortex.

Since the purpose of this dissertation was re-examination of the two psychological hypotheses (i.e. the visuo-spatial WM separation and the attention based rehearsal of spatial WM), the neural substrate of WM and how they represent WM contents are outstanding questions of this study. However, further study has to be conducted to investigate these problems. WM has been assumed as central function of our cognition, thus many researchers from psychologist to neuroscientist have taken keen interest in this cognitive system. In addition, many sophisticated techniques to analyze neural data have been developed recently (e.g.

multi-voxcel pattern analysis of functional imaging data). Future study employing these techniques will extend our knowledge for the neural mechanism of WM, and these findings will also offer new insight to psychological study intending to build functional model.

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