Investigating Visual Working Memory

Electrophysiological Delay Activity and Plasticity of Selection Mechanisms

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Part of this work is also included in articles already published or under review. Notably, Experiment 2 was published as Arend and Zimmer (2011) and Experiments 3 is submitted for publication as Arend and Zimmer (2012). In order to warrant a smooth reading, the respective passages are not marked in the text. Furthermore, in keeping with the practice of these articles, in the main text I consistently employ “we” instead of “I”.

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List of Abbreviations

°	Degree
€	Euro
%	Percent
$\eta^2_{partial}$	Effect size for ANOVAs with repeated measurements (partial η^2)
ε	Greenhouse-Geisser epsilon
µV	Microvolt
ANOVA	Analysis of variance
CDA	Contralateral-delay activity
cf.	Compare
D	Distractors
df	Degrees of freedom
EEG	Electroencephalography/Electroencephalogram
e.g.	For example
EOG	Electroocculogramm
ERP	Event-related potential
F	Test statistic from F distribution
fMRI	Functional magnetic resonance imaging
Hz	Hertz
IPS	Intraparietal sulcus
IT	Inferiror-temporal lobe
ms	Millisecond
p	Probability of equally extreme test statistic, given null hypothesis is true
p_{corr}	Greenhouse-Geisser corrected p-value
PPC	Posterior-parietal cortex
r	Pearson product-moment correlation coefficient
ROI	Region of interest
s	Second
t	Test statistic from Student’s t distribution
T	Targets
V1-4	Visual areas 1-4

Abstract

Visual working memory (WM) processes can be investigated via the so called change detection task. In a version of this task, the lateralized change detection task, two item arrays are presented, one on each side of the display. Participants have to remember the items in the relevant hemifield and to ignore the items in the irrelevant hemifield. From the electroencephalogram recorded while items are maintained in visual WM, slow potentials over posterior recording sites can be extracted. Additionally, a difference wave between contralateral and ipsilateral slow potentials with respect to the relevant items, the contralateral delay activity (CDA), can be calculated. As its amplitude varies with the number of items held in visual WM and reaches its asymptote with visual WM capacity, it is considered a pure neural correlate of visual WM load.

In the current work we pursued two main aims. Firstly, we set out to get a better understanding of the meaning of contralateral and ipsilateral posterior slow potentials and their contribution to WM maintenance. In Experiment 1, we examined whether the electrophysiological components, posterior slow potentials and CDA are sensitive for improvements of visual WM efficiency. Via an incentive manipulation we increased participants' visual WM performance. Interestingly, improved maintenance under incentives was reflected in the pattern of contralateral and ipsilateral slow potential activity, but not in the CDA. Interestingly, in Experiment 1 load-dependent activity emerged also over the hemisphere ipsilateral to the relevant hemifield, suggesting that the ipsilateral hemisphere is also involved in memory-related processes. This ipsilateral activity might either reflect a bilateral processing of relevant or else a lateralized processing of irrelevant, to-be-filtered-out, items. As in the lateralized change detection task the number of items on both sides of the display is typically identical, it was not possible to decide between these alternatives yet. In order to disentangle the influence of relevant and irrelevant items, in Experiment 2, we orthogonally varied the number of both types of items. Processing of relevant items caused purely contralateral load-dependent activity. Ipsilateral delay activity was solely caused by the irrelevant items. However, this was only the case if only one relevant item was to be maintained in visual WM. This suggests that whether irrelevant items are processed or filtered out depends on visual working memory load.

The second main issue of the current work was about the importance of competent selection mechanisms in the service of efficient visual WM functioning. In Experiment 3, we aimed to

selectively train participants' selection mechanisms to enhance visual WM efficiency. As visual WM has a highly limited capacity, efficient selection mechanisms are crucial for its successful functioning. Filter efficiency in visual WM can be measured by adding distractors to the memory and test array of the lateralized change detection task. As the amplitudes of contralateral slow potentials and CDA reflect the number of remembered items, one can infer whether distractors were filtered out. Filtering in the change detection task is assumed to happen via allocation of selective attention. Efficient selection via selective attention is also highly important in multiple object tracking (MOT). We trained participants' filter ability with the aid of this latter task. We observed large and long-lasting training induced improvements in MOT and present converging evidence that these improvements were specific to filter ability. However, training effects did not transfer to improved selection mechanisms in the change detection task. Instead, suggestive evidence indicates an overall improvement in selection mechanisms in the change detection task for both training and control group. Apparently, there exist subtle but substantial differences in the exact nature of filter mechanisms operating in change detection and MOT.

In a further analysis of the training data several further issues were explored. Firstly, an analysis on pure-target trials revealed contralateral as well as ipsilateral load-dependent delay activity and hence replicated the data pattern of Experiment 1. Secondly, as existing research assigns the prefrontal cortex a crucial role in regulating access to visual WM, the contribution of prefrontal cortex for filtering in the change detection task with distractors was investigated. For distractor-present conditions as compared to conditions without distractors, increased activity over the prefrontal cortex was observed.

Part 1

Visual Working Memory

1 Introduction into Visual Working Memory

1.1 The Concept of Working Memory

Imagine, you are cooking and you just cannot remember if you already added salt to the dish. Or you are going into your home office and when arriving, you have completely forgotten why you have gone there. Or you are standing in a warehouse in front of several suitcases and are trying to imagine the size and shape of your car boot to decide which of the suitcases fits well. These are all examples of everyday observations of (mal)functioning working memory (WM) which we all experience from time to time. WM is a system that maintains a small amount of information, despite its physical disappearance, in an active state over a short period of time. This information, kept online “in mind”, is also available for further processing or manipulation. WM is highly capacity-limited and this limit varies strongly between individuals (e.g., Kane, Bleckley, Conway & Engle, 2001; Luck & Vogel, 1997; Oberauer, Süß, Wilhelm, Wittmann, 2003).

WM is a key determinant for human cognition and plays a central role in many cognitive tasks. WM processes enable the temporal maintenance and manipulation of information, skills that form the basis of most higher cognitive functioning, such as language acquisition, reading comprehension, reasoning, problem solving, decision making and mental arithmetic. As WM constitutes a fundamental component for higher cognition, it is not surprising that individual differences in WM capacity are predictive for performance differences in many cognitive tasks as well as differences in measures of fluid intelligence (e.g, Cowan, Fristoe, Elliott, Brunner, & Saults, 2006; Daneman & Carpenter, 1980; Engle, Kane, & Tuholski, 1999; Kane et al., 2001; Kyllonen & Christal, 1990). In line with its predictive utility for many cognitive tasks, WM functioning is often considered as a stable cognitive trait (c.f., e.g., Engle, 2010; Perez & Vogel, 2011).

Sometimes, a differentiation between WM and short-term memory (STM) systems is made. STM is defined as a passive store for information whereas WM was originally introduced as a system not only responsible for passive storage, but the additional manipulation of stored information. Here, we share the view of contemporary WM-models (e.g., Luck, 2008; Postle, 2006; Zimmer, 2008), that the two systems are no competitors. Instead, STM can be seen as the storage part of the more enfolding and widespread concept of WM. The passive storage component of WM is the focus of the current work.

As we are interested in the storage of visual information, in the following we shortly review evidence for a subdivision of WM into part systems specialized for processing certain types of information. Thereafter, we will give a short overview over brain areas associated with visual WM functions.

1.2 The Subdivision of Working Memory

Converging evidence indicates separate WM stores for verbal and visual information. Firstly, examinations in brain damaged patients have shown double dissociations between visual and verbal WM stores. Certain patterns of brain damage disrupt WM for verbal information while WM for visual information remains intact and vice versa (De Renzi & Nichelli, 1975). Secondly, dual-task investigations provided additional evidence for the existence of separate storage systems for verbal and visual material. Processing verbal material in a secondary task had no impact on the main task of storage of visual information and vice versa, whereas using the same type of material in the secondary as well as the main task led to interference (see Repovs & Baddeley, 2006 for a review). Further evidence for a dissociation of visual and verbal WM comes from functional magnetic resonance imaging (fMRI) studies (e.g., Rodriguez-Jimenez et al., 2009) as well as electrophysiological (EEG) studies (e.g., Ruchkin, Johnson, Grafman & Canoune., 1997).

By contrast, the subdivision of separate WM stores for visual and spatial information is rather controversial. Here too, supportive evidence for a double dissociation for the storage of visual and spatial information comes from dual-task studies, where performance in a visual memory task is not interrupted by a spatial secondary task and vice versa whereas a secondary task using the same information type lowers performance in the main task (e.g., Della Sala, Gray, Baddelay, Allamano & Wilson, 1999; Logie & Marchetti, 1991; Woodman

& Luck, 2004). Furthermore, studies with brain damaged patients show that visual WM can be disrupted without limitations in spatial WM and vice versa (e.g., Della Sala et al., 1999; Farah, Hammond, Levine & Calvanio, 1988). Additionally, single unit recordings in monkeys (e.g., Wilson, O Scalaidhe & Goldman-Rakic, 1993), fMRI studies (e.g., Belger et al., 1998) as well as EEG studies (e.g., Mecklinger & Pfeifer, 1996; Mecklinger & Müller, 1996) have provided evidence for a dissociation of visual and spatial WM storage places. However, other evidence speaks against a clear separation in spatial and visual subsystems. For example, Zimmer and Lehnert (2006) report that visual WM for shapes is impaired when the spatial configuration of the shapes is changed from memory to test array, even if the location information of the shapes is completely irrelevant. Furthermore, Jiang, Olson and Chun (2000) reported that completely removing the context information, that means all but one to-be-compared object, from memory to test array, impairs visual WM performance.

1.3 Brain Areas Associated With Visual Working Memory

The neural substrates of visual WM have been investigated with the aid of single unit recordings in monkeys and neuroimaging studies in humans.

In match-to-sample tasks, an object must be remembered and is after a short retention interval compared to a second object, whereby the subject has to decide whether both objects are the same or differ in at least one feature. Single unit recordings in monkeys have revealed a sustained increase in firing rate of neurons during the retention interval of these tasks (see Fuster, 1995 for a review). This sustained activity, also called *delay activity*, is interpreted as the neuronal mechanism for holding information in an active state after its physical disappearance. The interpretation that the observed delay activity is indeed specific to the process of maintaining information in WM and not just a reflection of task-general processes is supported by two observations. Firstly, delay activity in different cortical areas is specific to specific features of the maintained objects, such as their location or identity (e.g., Chafee & Goldman-Rakic, 1998; Chelazzi, Duncan, Miller & Desimone, 1998). Secondly, delay activity diminishes when the monkey failed to answer correctly (Funahashi, Bruce & Goldman-Rakic, 1989; Sakai, Rowe & Passingham, 2002). Three areas have crystallized out to be particularly relevant for storing information: The inferior temporal cortex, the parietal cortex and the prefrontal cortex. Delay activity in the inferior temporal cortex was shown to be sensitive for the identity of the objects (Chelazzi, et al., 1998; Miller, Li & Desimone, 1993). Contrary, delay activity in the LIP is specific for locations (e.g., Chafee & Goldman-Rakic, 1998; Constantinidis & Steinmetz, 1996). The prefrontal cortex has found to be active for both, object and location information (e.g., Rao, Rainer & Miller, 1997), but additionally coded more complex associations and abstract rules (e.g., Asaad, Rainer & Miller, 1998; Wallis, Anderson & Miller, 2001).

Analogous to single unit recordings, delay activity during WM maintenance has also been observed in fMRI studies in humans. Here too, during the retention interval of WM tasks sustained activity can be measured that is interpreted to possess a functional role for the active maintenance of information during the delay (e.g., Robitaille et al., 2010; Todd & Marois, 2004). Congruent with results of single unit recordings in monkeys, activity is diminished if memory is not accurate (Pessoa, Gutierrez, Bandettini & Ungerleider, 2002). Delay activity is mainly observed in the parietal, inferior temporal and prefrontal cortex. In accordance with observations in monkey studies, specific brain areas responsible for the maintenance of visual and spatial information have also been found in humans: Location-specific activity has been observed in the parietal cortex (Sereno, Pitzalis & Martinez, 2001); the inferior temporal cortex was shown to be sensitive for identity and features of an item (Druzgal & D'Esposito, 2001); the prefrontal cortex is responsible for complex control functions (for a review see Smith & Jonides, 1999).

Interestingly, delay activity has shown to scale with the number of representations in WM. As WM load increases, delay activity also increases (e.g., Cohen et al., 1997; Robitaille et al., 2010; Todd & Marois, 2004; Xu & Chun, 2006). Interestingly, some authors report that delay activity reaches an asymptote at about four items (e.g., Todd & Marois, 2004; Xu & Chun, 2006). This asymptote is in accordance with known WM capacity limits and therefore constitutes a further hint for the functional role of delay activity for WM (Todd & Marois, 2004; Xu & Chun, 2006).

The prefrontal cortex constitutes a crucial structure for WM functioning. Its exact role in WM maintenance, however, is hotly debated. The PFC might be involved in WM-storage proper or might merely be a pure control center (see, e.g., Postle, 2006; Zimmer, 2008). Disagreement between researchers also exists concerning the question of a dorsal-ventral division of PFC for spatial and visual information (see, e.g., Haxby, Petit, Ungerleider & Courtney, 2000; Levy & Goldman-Rakic, 2000, for the assumption of and, e.g., Wager & Smith, 2003, against the assumption of such a division). Furthermore, the PFC is assumed to be involved in a variety of executive functions, as for example, prevention of interference and distraction, attention, control and selection, motivation, reward expectancy, etc. Dorsal and ventral PFC regions might be subdivided according to the specific kind of executive processes needed for the task (Wager & Smith, 2003). As the current dissertation project focuses on the passive storage of visual information, we forgo a detailed analysis of the PFC in the service of WM (for a review, see Postle, 2006; Smith & Jonides, 1999; Wager & Smith, 2003). However, we will come back to prefrontal structures within the scope of the investigation of selection mechanisms in visual WM (see Chapter 13).

Interestingly, the brain structures for WM maintenance of visual and spatial information, as reviewed above, map the ventral and dorsal pathways for perception. These two pathways are two perceptual processing streams that predominantly code for object (ventral) and spatial (dorsal) information and end in the inferior temporal and parietal cortices, respectively (e.g., Goodale & Milner, 1992; Milner & Goodale, 2008). A dissociation between those processing streams was also shown for WM in fMRI (for a review, see Wager & Smith, 2003) and EEG studies (Mecklinger & Müller, 1996). This indicates that areas responsible for the processing of sensory information of objects also serve as the storage places of this information via sustained activity (for related theories, see, Jonides, Lacey & Nee, 2005; Postle, 2006; Zimmer, 2008).

Recent research, however, has presented data that is not in line with the division in PPC for spatial information and IT for identity information. Xu and Chun (2006) report that activity in the superior IPS, a structure within the parietal cortex (see Figure 1.1), is sensitive for the complexity of the to-be-maintained objects. This structure seems to code for detailed feature information (Xu & Chun, 2006, 2009). This finding is obviously not in conformity with research reviewed above, that the PPC is the storage place for spatial information. Maybe, the made classification of PPC for spatial information and IT for object information might be a bit imprecise under certain circumstances. It might be that further research has to work out neuronal areas that code for spatial information and areas that code for object information with a finer resolution.

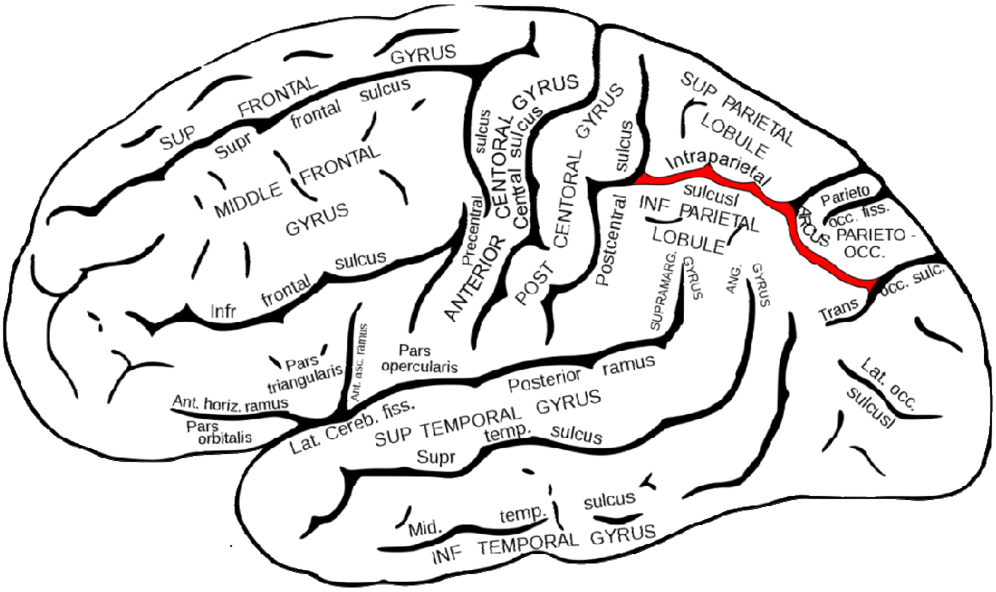

Figure 1.1. Illustration of the position of the intraparietal sulcus (IPS). From Wikimedia Commons (en.wikipedia.org/wiki/File:Gray726_intraparietal_sulcus.svg).

2 Measuring Visual Working Memory Functioning

2.1 Working Memory Tasks

A couple of tasks have been established to measure visual WM functioning. In simple span tasks, participants encode a sequence of stimuli which they have to maintain in memory for several seconds. Afterwards, the stimuli have to be recalled in the correct chronological order. As information has to be passively retained without additional processing demands, this task is a purely passive WM task. Visuo-spatial versions of this task are the Corsi task and the spatial span. Spatial locations are marked consecutively and thereafter participants' task is to correctly reproduce the serial order of marked locations by tapping or clicking on them.

Complex span tasks incorporate a storage as well as a processing component and are therefore to classify as active WM tasks. As in simple span tasks, participants have to store a sequence of stimuli in memory. However, after each storage stimulus, an additional processing task has to be performed. An example of a visuo-spatial processing component is the decision of whether presented patterns are symmetrical.

In the *n*-back task, participants see a sequence of stimuli, for example pattern matrices. Their task is to respond each time when the currently presented stimulus matches the one presented *n* trials before. Task difficulty increases with increasing *n*, because with large *n*s more items have to be maintained active and to-be-compared items are further afar from each other. The *n*-back task is an active WM task where information has to be compared and constantly updated.

In the change detection task, participants see a *memory array* of several objects, which they have to passively store in memory for a short *retention interval*. The duration of the memory array is usually up to several seconds. In the ensuing *test array*, in 50% of the trials, one object has changed one feature (*mismatch*), for example color or shape, in the remaining trials all objects remain the same (*match*). Participants have to indicate whether a change had occurred or not. As the change detection task is employed in the present work, we will examine it in more detail now.

2.2 The Advantages of the Change Detection Task as a Measure of Visual Working Memory Functioning

The properties of visual WM have been extensively examined via the change detection task (for a review see Luck, 2008). Its structure is simple and it is easily explainable to participants. Because of this simplicity, there is a more manageable number of cognitive processes during the performance of this task as compared to complex tasks such as the *n*-back task or storage and processing tasks. Necessary are processes of perception when the memory array is presented, consolidation and storage processes during the retention interval and retrieval and comparison processes during test (for a discussion of task-general processes such as effort or arousal, see Chapter 3). Furthermore, the type of retrieval used in this task is well suited to prevent response interference. Behavioral measures of visual WM maintenance are therefore less contaminated by other processes. The test array can be directly compared to the representation hold in memory. Contrary, in span tasks for example, the memoranda have to be reproduced in their serial order, whereby reproducing the first items might disturb the maintenance of the last ones. The result of this response interference would be an underestimation of WM capacity (see Luck, 2008, for a similar discussion). A further advantage is the flexibility and adaptability of the change detection task. Within one design-framework, one is able to investigate a variety of questions, which leads to a better comparability of gained results. Varying the number of presented objects, one can measure the capacity of visual WM; varying the complexity of presented objects, one can investigate the resolution of representations in visual WM; using masks, one can analyze consolidation processes; designing objects consisting of several features, one can examine the question of the storage-unit of visual WM, that is, bound objects vs. individual features; presenting relevant objects together with distractors, one can investigate the selection mechanisms of visual WM, etc. For the present work, the utilization of the change detection task to estimate visual WM capacity and examine selection mechanisms is of foremost importance.

Although at first glance, this task seems to be truly a visual WM task, it might be contaminated through verbal processes. Participants might recode visual object information into verbal labels. However, Luck and Vogel (1997) ran a control experiment to demonstrate that there is no contamination through verbal processes. They designed a dual-task, where participants remembered two digits and vocalized them at the end of the trial. While they were maintaining the digits in memory, they additionally performed a change detection task for colored squares. Performance for color-memory was not worse in this condition as compared to a condition without the verbal task. This indicates that no verbal memory processes are engaged in the visual change detection task.

2.3 An Index of Visual Working Memory Capacity

Visual WM is characterized through a highly limited capacity. From change detection performance for a different amount of to-be-remembered items – different *set sizes* – it is possible to estimate how many items a tested person is able to hold in visual WM (Cowan, 2001).

When N items are presented in the memory array of the change detection task and a person has a visual WM capacity of k items, then he or she is able to detect a change in 100% of the trials, when $k > N$. When $k < N$, he or she can hold k of the N items in memory and will consequently detect a change correctly with a probability of k/N; in the remaining $(1-k)/N$ trials, he or she guesses. If $N < k$, we talk about below-capacity set sizes, if $N > k$, above-capacity set sizes. Response accuracies are stable and nearly 100% for below-capacity set sizes, but decrease with increasing number of items for above-capacity set sizes. For example, if a person has a capacity limit of three items, and four items are to be maintained, the probability that he or she holds the one item, that changes in a mismatch case, is 0.75, whereas when five items are to be maintained the probability is only 0.6 etc.

To estimate a person's visual WM capacity the following formula can be employed: K = (Hits – False Alarms) * N, whereby K is the measured capacity, Hits are the number of correct mismatch responses, False Alarms are the number of erroneous mismatch responses and N is the number of to-be-remembered items (for the exact derivation of this formula, see Cowan, 2001). This so called *K-index* was developed by Pashler (1988) and further developed by Cowan (2001) and is an index of visual WM capacity. Importantly, this measure, contrary to the mean accuracies, abstracts from a specific set size. When applying this formula for above-capacity set sizes, one obtains an estimate of a person's individual working memory capacity. The K-index has proven to be a valid measure of visual WM capacity. In several experiments it was quite constant across larger set sizes, up to 8-10 items (Cowan, 2001; Fukuda & Vogel, 2009; Vogel & Machizawa, 2004).

Importantly, it only makes sense to interpret the K-index for above-capacity set sizes. As it constitutes a measure to estimate participants' visual WM capacity, staying below their capacity is obviously pointless. For example, a person has a visual WM capacity of k=5 and hence 100% correct trials for set sizes two and three. Calculating the K-index would lead to a K = 2 for set size two and a K = 3 for set size three. Both measures underestimate the actual capacity. As, per definition, the obtained K can only be as high as the maximal set size used, one has to be careful to exceed all participants' WM capacities. For below-capacity set sizes, calculating the K-index, would lead per definition, to a significant effect of the number of set size, as seen in the example. It occurs even when participants perform equally well for various set sizes and is not interpretable.

We decided to apply mean response accuracies as well as the K-indices as dependent measures of interest. We use mean response accuracies to test for set size effects and interactions with set size and the K-indices to obtain an estimate of WM capacity limits. We defined K_{max} as the highest value from among all Ks that were calculated for the different set sizes employed in the respective experiment.

The K-Index implies that visual WM consists of a certain amount of slots. When we say a person can maximally store *k* items in visual WM, this implies that we assume some kind of slots. Each slot comprises the storage of one item and persons differ in the number of slots they have at their disposal. This leads to the question of what exactly is stored within one slot. Data of Luck and Vogel (1997) strongly speak for an object-based storage in visual WM, where multiple features are bound together to and stored as integrated-object files. However, other evidence conflicts with the idea of object-based storage in visual WM (e.g., Delvenne & Bruyer, 2004; Olson & Jiang, 2002; Wheeler & Treisman, 2002). In particular, there are observations that increased object-complexity is not “for free” and comes along with decreased numbers of stored objects (Alvarez & Cavanagh, 2004).

Unfortunately, also the question if visual WM is really built of discrete slots for a limited amount of items or if we can principally store any number of items but with different resolution is still an unresolved issue. According to the latter view, as the number of items increases, the amount of resource for every single item decreases leading to a poorer resolution of its representation. Recent research suggests that the number of maximally storable objects is limited to about four (e.g., Awh et al., 2007; Luck & Vogel, 1997; Xu & Chun, 2009). However when the resolution required for resolving all object features is high, this additional constraint diminishes measured capacity (e.g., Alvarez & Cavanagh, 2004; Xu & Chun, 2009). The number of slots a person has at his or her disposal, but not the resolution of the representations, is predictive of measures of fluid intelligence (Fukuda, Vogel, Mayr & Awh, 2010) whereas the available resolution for representations, but not the number of overall available representations, can be enhanced by perceptual expertise (Scolari, Vogel & Awh, 2008).

Although the detailed understanding of the exact nature of stored representations in visual WM is a crucial question, we will not go into further detail because this question is only tangent to the topic of the dissertation project (for a broader discussion see, e.g., Alvarez & Cavanagh, 2004; Luck, 2008; Xu & Chun, 2009; Zimmer, 2008).

Part 2

Electrophysiological Delay Activity in the Lateralized Change Detection Task

3 Electrophysiological Online-Measures of Visual Working Memory

Behavioral measures of visual WM functioning can be supplemented by simultaneous electrophysiological recording which provides an online measure of working memory processes. In line with neuroimaging results reported above (Chapter 1.3), sustained activity during visual WM maintenance can be extracted (slow potentials). These slow potentials can be measured during the retention period of the change detection task (e.g., Rämä et al., 1997; Ruchkin, Johnson, Grafman, Canoune & Ritter, 1992; Ruchkin, Canoune, Johnson & Ritter, 1995; Mecklinger & Pfeiffer, 1996). Their amplitudes increase with visual WM load (e.g., Rämä et al., 1997; Ruchkin et al., 1992; Ruchkin et al., 1995; Mecklinger & Pfeiffer, 1996). This observation constitutes important evidence for the claim that these slow potentials reflect the maintenance of items in visual WM.

However, these slow potentials might be contaminated by non-mnemonic processes, such as perception of the items or task-general processes of effort, arousal, anticipation of the test stimulus, or preparation for an upcoming response. These variables also might be responsible for an increase in slow potential amplitudes with increasing number of to-be-remembered items (McCollough, Machizawa & Vogel, 2007; Vogel & Machizawa, 2004).

The *contralateral control method* (Gratton, 1998) provides the opportunity to circumvent this problem and to extract the process of interest—the maintenance process in the present case—from other task-general processes. In the *lateralized change detection task*, the same amount of items is presented in two arrays located to the left and the right of the center of the screen, respectively. Participants are cued which array is relevant in a given trial, but are instructed to remain fixation on the center of the screen. Only the cued items – the relevant items – have to be remembered. Due to the contralateral organization of the visual system (see Figure 3.1A), visual information from the relevant items is first processed in the hemisphere contralateral to the relevant hemifield while information from the irrelevant items is first processed in the hemisphere ipsilateral to the relevant hemifield which is of course contralateral to the irrelevant hemifield. In the following, *contralateral activity* always refers to neural activity that is observed over the hemisphere that is contralateral to the relevant hemifield and consequentially receives the relevant items (first) and *ipsilateral activity* always refers to neural activity that is observed over the hemisphere that is ipsilateral to the relevant hemifield and consequentially receives the irrelevant items (first). The general logic is that all task-general processes as perception or effort should elicit bilateral activity. However, the process of maintaining the relevant items in memory should be restricted to the contralateral hemisphere with respect to the side of the relevant array. The amount of additional contralateral activity should therefore mirror this process of interest.

Klaver, Talsma, Wijers, Heinze & Mulder (1999) further developed the contralateral control method to isolate the process of maintaining information in visual WM. Participants performed a change detection task with polygons. Two memory arrays containing one polygon each were presented for 1000 ms, one to the left and one to the right of the center of the screen. Participants were instructed to fixate the center of the screen and a peripheral cue indicated the relevant memory array. During the retention period, the authors observed a large slow potential over occipital recording sites. This slow potential was more pronounced over contralateral as compared to ipsilateral recording sites. The authors concluded that the lateralized presented stimulus was maintained in the contralateral hemisphere.

4 Contralateral Delay Activity (CDA)—A Purified Electrophysiological Measure of Representations in Visual Working Memory

Vogel & Machizawa (2004) refined this technique in order to extract pure memory related activity. In their version of the lateralized change detection task, participants fixate the center of a bilateral display of items and are centrally cued which side to maintain in memory. The same amount of items is briefly presented in both hemifields (100 ms). Using this short interval, the authors intended to prevent eye-movements of participants towards the relevant items; this is important because the fixation of objects in the relevant hemifield would result in a bilateral processing of these objects. Throughout the retention interval of the lateralized change detection task, a posterior sustained negative slow potential over the hemisphere contralateral to the relevant hemifield was observed (Vogel & Machizawa, 2004; McCollough et al., 2007), similar to the one observed by Klaver et al. (1999). According to the general logic of the contralateral control method (already introduced above), task-general processes should show up bilaterally, whereas the process of maintaining the relevant items in memory should be restricted to the contralateral hemisphere. The additional contralateral activity should therefore mirror this process of interest. By computing a difference wave, that means, by subtracting ipsilateral from contralateral activity, the non-specific activity should be subtracted out (McCollough et al., 2007). Although both this difference wave and contralateral slow potentials are delay activity over the contralateral hemisphere, in order to differentiate between both measures, we here reserve the term *contralateral delay activity (CDA)* for the difference wave.

The CDA (see Figure 3.1B) is a negative component with a maximum over occipital and posterior parietal recording sites. It starts about 300 ms after onset of the memory array and lasts until the end of the retention period whose duration is usually 900 ms. This component was observed for different types of visual features, such as colors (e.g., Vogel & Machizawa, 2004), orientations (e.g., Vogel et al., 2005) and shapes (e.g., Luria & Vogel, 2010). Even in versions of the task with a retention period of up to three seconds the CDA was present during the whole retention interval (McCollough et al., 2007).

4.1 The CDA as a Pure Neural Correlate of the Amount of the Number of Representations in Visual Working Memory

In a lateralized change detection design in which the number of items was systematically varied, Vogel and Machizawa (2004) observed an increase in CDA amplitude with increasing number of items. The authors concluded that the CDA is a probable candidate to reflect the amount of items maintained in visual WM. In line with this reasoning, the CDA amplitude was significantly smaller for trials with incorrect responses as compared to trials with correct responses (Vogel & Machizawa, 2004). As task-general processes are thought to be subtracted out, the CDA might be the better—namely purer—measure of visual WM as compared to the posterior slow potentials. However, before accepting the CDA as a pure measure of the number of representations in visual WM, alternative hypotheses have to be excluded.

Excluding alternative hypothesis1: Task-general processes such as effort or arousal

The slow potentials might partially reflect non-mnemonic task-general processes. This constitutes a problem in interpreting them as a measure of visual WM processes, as detailed above. The contralateral control method should resolve this problem in that the CDA is extracted as a pure reflection of visual WM processes. However, the same problem already mentioned in the context of the slow potentials might also apply to the CDA. Together with the increasing number of to-be-remembered items also executive demands or task-general processes such as overall task difficulty, effort or arousal might increase (Vogel & Machizawa, 2004). The CDA might equally well be influenced by these processes. To exclude this possibility, Vogel & Machizawa (2004) have run conditions with above-capacity set sizes. They presented their subjects trials with up to 10 to-be-remembered items. Their reasoning was the following: If, on the one hand, task-general processes as listed above are at least in part responsible for the increase in CDA amplitude with increasing set size, CDA amplitude should be a function of the number of items regardless if visual WM capacity is reached, because these factors should increase also for above-capacity set sizes. If, on the other hand, the CDA is a neural correlate of visual WM maintenance, its amplitude should increase only until visual WM capacity is reached, that is at three to four items, and should not further increase for above-capacity set sizes. They observed the latter result pattern. CDA amplitude increased from one to two to three items, where it reached its asymptote. For these reasons, the CDA’s amplitude is thought to directly reflect the amount of items kept in visual WM.

Excluding alternative hypothesis 2: Perceptual processes

Increasing the number of to-be-remembered items in the display increases perceptual demands. To show that the level of CDA amplitudes does not reflect these perceptual demands, Ikkai; McCollough & Vogel (2010) parametrically manipulated the number of to-be-remembered items and the perceptual requirements of these items. Participants performed the lateralized change detection task for colored objects under easy as well as difficult perceptual conditions, by reducing the contrast of colors in the latter one. This resulted in an orthogonally varied design with set sizes two and four under high and low contrast. Observed CDA amplitudes were exclusively modulated by the variation of the to-be-remembered items, irrespective of the perceptual requirements. This is clear indication that the CDA is a measure of the number of representations in visual WM and independent of perceptual demands.

Excluding alternative hypothesis 3: The size of the zoom lens of attention

An additional caveat can be issued concerning the interpretation of the CDA as an electrophysiological correlate of memory load, because the spatial extent of the memory array is usually confounded with the number of objects. The more to-be-remembered objects are presented in the display, the larger is the spatial extent of the task-relevant region and therefore the required size of zoom-lens of attention. Therefore, the CDA might be a neural correlate of the distribution of spatial attention in the display as well. To weaken this argument, McCollough et al. (2007) presented two or four to-be-remembered objects in two conditions: They either lay close together or were far apart from each other. This resulted in a 2 × 2-design with an orthogonal variation of number of items and distance. The resulting CDA amplitude was solely manipulated by the number of items and completely unaffected by the amount of space the items take up. This provides important evidence for the fact that the CDA is not solely a marker of the expanse of the attentional zoom lens.

Excluding alternative hypothesis 4: The number of attended locations

Ikkai, McCollough & Vogel (2010) sequentially presented their participants two memory arrays, each with two colored items, resulting in a total number of four to-be-remembered objects. In one condition all four items had a different location on the display, in the other condition, the two items in the second memory array covered exactly the same location as the two items in the first memory array. This design allowed differentiating between the hypothesis that the CDA only reflects the number of locations stored in visual WM and the hypothesis that the CDA reflects the number of items represented in visual WM. In line with the latter hypothesis, CDA amplitude was a function of the number of to-be-remembered items, irrespective if they covered the same locations in the display or not.

To sum up, data collected till now converge to the straightforward view that the CDA reflects the amount of representations in visual WM.

4.2 Interindividual Differences in Visual Working Memory Capacity

Persons differ in their visual WM capacity. If the CDA is sensitive to the amount of items hold in visual WM, then it should also mirror the capacity limit of an individual. If so, for a person who is able to hold only two items in visual WM, CDA amplitude should reach its asymptote faster than for a person who is able to hold four items in memory. However, comparing ERPs of different persons is always accompanied with problems (see, e.g., Luck, 2005). In order to use the CDA as a measure of individual differences, Vogel and Machizawa (2004) calculated the amplitude difference between two and four items. They reasoned that if, on the one hand, a person has a low capacity of for example about two items, that person would in both conditions hold only two items in memory. Consequently, there should be no large increase—or even no increase at all—in CDA amplitude from two to four presented items. On the other hand, a person with high capacity of, for example nearly five items, should have a CDA amplitude far away from its limit for two items and show a considerable increase in amplitude from two to four items. Indeed, the authors observed a large positive correlation between individual memory capacity, measured with the aid of the K-Index and the CDA amplitude increase between two and four items.

4.3 What Information Might be Coded by the CDA

Location information: A spatial pointer system

It seems very plausible that the CDA codes spatial information about the locations of the objects (e.g. McCollough et al., 2007). In line with the organization of the visual system the CDA is contralateral in nature, indicating its sensitivity for object locations. Additionally, it emerges over posterior recording sites. This indicates that its neuronal sources are, at least in part, retinotopically organized (McCollough et al., 2007). McCollough et al. (2007) hypothesized that the CDA might act as a spatial pointer towards targets. Considering the results of Ikkai et al. (2010) this would imply that two spatial pointers can be directed towards two objects at the same position.

This idea is further supported by findings of a CDA in the tracking phase of a lateralized version of the multiple object tracking (MOT) task. In this task, several identical objects, usually circles, are presented on the screen. Some objects, the targets, are highlighted for a short time to distinguish them from the distractors. Afterwards, all objects, now indistinguishable again, move for several seconds within a defined array. Participants' task is to track the targets and ignore the distractors. When the objects stop moving, participants have to indicate the targets. The CDA amplitude, measured during the tracking period of a lateralized version of this task, is dependent on the number of tracked targets (e.g., Drew & Vogel, 2008; Drew, Horowitz, Wolfe & Vogel, 2011). As all objects, targets and distractors, actually look alike during the tracking phase of MOT, only object-locations constitute a valid criterion for their differentiation. The CDA might reflect a process that works as a spatial pointer towards the relevant object locations. Consequently, when more locations have to be tracked, the amplitude of the CDA increases. Drew et al. (2011) directly compared the CDA in the lateralized change detection and the lateralized MOT task within the same participants. The amplitude of the CDA in MOT was more pronounced as compared to the amplitude of the CDA in the change detection task (Drew et al., 2011). One part of the CDA was observed in both tasks. It had a similar topography and its amplitude varied with the number of tracked or maintained items. The additional CDA-activity in MOT was more dorsally distributed and showed no modulations with the number of tracked items. The authors interpreted the additional CDA-activity in MOT as an updating mechanism for changing target positions. The common CDA-activity for MOT and change detection was interpreted as reflecting an indexing or pointer-system towards a limited number of relevant objects (Drew et al., 2011).

Feature information

As just outlined, the CDA might code for object locations. McCollough et al. (2007) even discuss that identity information of the objects might not at all be coded in the CDA. However, further research has indicated that the CDA codes some kind of feature information of the objects. Woodman and Vogel (2008) presented their participants two or four colored bars with different orientations in a lateralized change detection task. Participants' task was either to remember the color or the orientation of these objects. Although they processed exactly the same visual input—the colored bars—the amplitude of the CDA depended on the specific task they performed; it was higher in the orientation condition as compared to the color condition. This experiment indicates that some form of object information is reflected in the CDA (cf., Perez & Vogel, 2011). However, how much object information is coded by the CDA and the precise nature of this object information remains to be determined.

Above (Chapter 2.3) we shortly discussed whether the storage units of visual WM are individual features or bound objects. The CDA seems to reflect a pure measure of the number of items in visual WM and seems not to be contaminated by other task-general processes, requirements that might make it a suitable measure for the investigation of this question. However, if the CDA will crystallize out to reflect only a spatial pointer towards object locations, as discussed above, it is actually not at all sensitive for this sort of research questions. Using stimuli that consist of several features, and observing a CDA amplitude that is modulated as a function of the number of objects and not as a function of the number of features, can mean two different things. Firstly, it might indicate that bound objects are stored in visual WM. Secondly, it might only mirror the fact that the CDA is not sensitive for object features. A recently published study (Luria & Vogel, 2010) nevertheless used the CDA as an indicator of the storage-unit. Based on CDA amplitudes the authors concluded that bound objects rather than individual features are stored.

4.4 Neuronal Underpinnings of the CDA

The intraparietal sulcus (IPS; see Figure 1.1) is treated as a possible neuronal source of the CDA (e.g., Robitaille, Grimault & Jolicoeur, 2009, Robitaille et al., 2010; Perez & Vogel, 2010). Firstly, the CDA’s maximum lies over posterior parietal and occipital recording sides (McCollough et al., 2007). Secondly and most convincing, neuroimaging data consistently show that the IPS behaves in line with what would be anticipated from a brain structure underlying the CDA. In the retention interval of change detection tasks with visual material, activity in the IPS increases parametrically with the number of to-be-remembered items. Importantly, activity increases in the IPS reach an asymptote for four items, that is, within limits of visual WM capacity (Linden et al., 2003; Mitchell & Cusack, 2008; Todd & Marois, 2004; Todd & Marois, 2005; Robitaille et al., 2010; Xu & Chun, 2006). Furthermore, interindividual differences in activity increases in the IPS with increasing visual WM load have shown to be predictive of visual WM capacity (Todd & Marois, 2005). This result too, is in line with properties of the CDA. As reported above (Chapter 4.2), interindividual differences in increases in CDA amplitude with load also are predictive of visual WM capacity (Vogel & Machizawa, 2004).

As the IPS potentially constitutes a neuronal generator of the CDA, the question arises what process might be reflected by the IPS activity. Several lines of evidence indicate that activity in the IPS (in particular the inferior IPS) reflects a spatial pointer towards relevant objects. Firstly, load-sensitive activity in the IPS is also observed during the tracking period of the MOT task (e.g., Culham, Cavanagh & Kanwisher, 1998; Jovicich, et al., 2001). Secondly, Xu and Chun (2006) showed that during the retention interval of a change detection task, activity in the inferior IPS was sensitive for the number of to-be-remembered objects only and not for additional feature information of the objects. Consequently, activity in the IPS might reflect a spatial pointer system that contributes to the generation of the CDA in the lateralized change detection task. In that it might accomplish the purpose to maintain the target locations over the maintenance period.

The observations that activity in the IPS scales with set size and reaches an asymptote with memory capacity—all observations that also apply to the CDA—were taken as indication that the IPS might be a generator of the CDA. However, there are also data challenging this view. All, except one, of the studies mentioned above that examined the IPS in the change detection task, employed central displays and obtained bilateral IPS activity during the maintenance phase. Only Robitaille et al. (2010) employed a lateralized change detection task. They reasoned that with this design they might observe a CDA-like contralateral activation in the IPS. In the same participants, they recorded EEG, MEG and BOLD responses during the task. Although the authors obtained an electrophysiological CDA and also lateralized magnetic activity, BOLD responses in the IPS were bilateral. At first glance, this result is not in line with a contralateral bias in the electrophysiological data. It is difficult to imagine how a contralateral observed electrophysiological component can stem from a bilateral neuronal source. The authors discuss that if the memory trace is initially lateralized but becomes bilateral over time, because of their poor temporal resolution, fMRI data might not be capable of revealing the lateralized effects. In line with the reasoning that the memory representation might become bilateral over time, McCollough et al. (2007) discuss a diminution of the CDA at the end of the retention interval as a consequence of an increase in ipsilateral activity (for further discussion see Chapter 17 in the General Discussion). However, Robitaille et al. (2010) additionally discuss that perhaps the used methods reflect slightly different processes that contribute to a successful maintenance of item information in visual WM. In that case, the IPS would not constitute a neuronal source of the CDA. Unfortunately, Robitaille et al. (2009) did not clearly replicate the CDA, but obtained it only for one hemisphere. Contrary, there was a clear bilateral EEG as well as MEG signal in their data. Consequently, their conclusion that IPS activity as measured via fMRI might not be a neuronal source of the CDA might be a bit premature. Further indication for Robitaille et al.'s (2009) assumption, however, comes from a recently published study of Cutini, Scarpa, Scatturin, Jolicoeur, Pluchino, Zorzi and Dell'Aqua (in press). Using near-infrared spectroscopy (fNIRS) the authors recorded hemodynamic responses during the retention interval of a lateralized change detection task for colored stimuli. Here again, in accordance with the above reported results, the hemodynamic responses were bilateral and not lateralized, as would be expected from a CDA-generator. These results are further indication against the assumption that the activity in the IPS and the electrophysiological CDA, both measured during the retention period of the change detection task, reflect a common neural process.

As already discussed in the preceding chapter (Chapter 4.3), the CDA might reflect several processes that contribute to the successful maintenance of objects in visual WM. We discussed that it might reflect a spatial pointer towards the object locations, but it might additionally carry some object information. In line with this reasoning, McCollough et al. (2007) discuss that the CDA is likely to have several generators. They even speculate that frontal structures might contribute to the generation of the CDA. To conclude, it is the assignment of further research to crystallize out which neuronal sources contribute to the CDA. To date, besides challenging results, there are also some indications that the IPS might constitute a CDA-generator. If these turn out to be valid, the IPS might reflect a pointer-system that maintains the relevant object locations active during maintenance. We will come back to this issue in the General Discussion (see Chapter 20.1.2).

To conclude, the change detection task seems to constitute a valid approach to investigate visual WM functioning. The CDA, extracted from the EEG measured during the retention interval of the lateralized version of this task, is apparently a pure measure for the amount of representations in visual WM. Therefore, in the following, we will employ the lateralized change detection task and the CDA to gain a deeper insight into visual WM functioning.

5 Experiment 1: Plasticity of Visual Working Memory—Behavioral and Electrophysiological Evidence for Incentive Effects

5.1 Introduction

In Experiment 1 we pursued two aims. Firstly, we evaluated the lateralized change detection task and the during its retention interval measurable electrophysiological components with respect to their suitability for the current dissertation project. At the beginning of the dissertation project the CDA as a measure of visual WM load had not yet been replicated by others than the working group of Vogel (Vogel & Machizawa, 2004; Vogel, McCollough & Machizawa, 2005; McCollough et al., 2007). Therefore, in the present experiment we employed the lateralized change detection task for a varying amount of colored items, similar to the task employed by Vogel and Machizawa (2004). We examined whether a CDA is extractable during the retention period of this task and whether its amplitude is sensitive for load-manipulations. Furthermore, we were interested in influences of load-manipulations on the two building blocks of the CDA, the contralateral and ipsilateral slow potentials.

One main topic of the dissertation project is the investigation of visual WM plasticity through training (see Part 3). For this training study, we planned to measure visual WM processes via the lateralized change detection task and analyze training effects on the posterior slow potentials and the CDA. Therefore, the second aim of Experiment 1 was to determine whether the lateralized change detection design as well as the associated electrophysiological components, CDA and slow potentials, are in principle suitable to measure effects of visual WM plasticity. Therefore, in the current experiment, we intended to induce a short-term increase in participants' visual WM performance through the anticipation of performance-dependent monetary incentives. In order to measure potential performance improvements, we ran two conditions: We compared a baseline condition in which participants did not receive any incentives with an incentive condition in which they were paid based on their performance.

There is a considerable body of literature on reward-anticipation and the dopaminergic and limbic system as the neural bases of incentive processing. However, what we are specifically interested in, is the question in how far the anticipation of reward affects a more efficient employment of available cognitive resources and thereby leads to an improved visual WM functioning. Research on this question is rare and results are mixed. Szatkowska, Bogorodzki, Wolak, Marchewka and Szeszkowski (2008) found no behavioral incentive-improvements on a 2-back verbal WM task. Furthermore, Shiels et al. (2008) tested children with ADHD and found only incentive-related improvements in a backward-span task which demanded storage and manipulation and not in a forward-span task which demanded storage only. However, having a closer look on their performance data, even the reported effect seems not to be an actual incentive-effect. When the incentive condition followed the baseline condition, there were no differences in performance between the two conditions. The observed "incentive" effect rather seems to be driven by a heavy decline in performance when the baseline condition follows the incentive condition. Apparently, in that case the amount of effort the children invested in the task collapsed in the baseline condition as compared to the preceding incentive condition. Positive effects of incentives on a working memory task are reported in a study using behavioral as well as pupillometric data as indicators of effort. Pupil sizes increase with increasing effort. Subjects performed a reading span task and effort was manipulated through incentives. Both, performance accuracy as well as pupil sizes increased with incentives (Heitz, Schrock, Payne & Engle, 2008). In a visual WM task with distractors reaction times increased and activity in visual association cortices as well as frontal areas was modulated under incentives. (Krawczyk, Gazzaley & D'Esposito, 2007). Participants in the study of Small et al. (2005) performed a variant of the Posner-task, a spatial attention task, under conditions with or without incentives. Activation in posterior regions which are associated with spatial attention was enhanced under incentives.

An improvement in visual WM performance under incentives should be reflected in response accuracies. Furthermore, K_{max}, the measure of visual WM capacity, should increase. The crucial question is whether such an improvement can also be observed in the electrophysiological components examined here.

Rösler, Heil and Röder (1997; see also e.g., Khader, Schicke, Röder and Rösler, 2008) reason that the amplitude of slow potentials varies as a function of *cognitive effort*. When participants spend more effort on a task, the amplitudes increase (Rösler, et al., 1997). Therefore we expect that posterior slow potentials' amplitudes are higher under incentives as compared to the baseline condition. Actually, this result pattern might have two implications, because increasing effort might influence slow potential amplitudes by two different mechanisms: Firstly, participants might endeavor to solve the task better than in the baseline condition. They invest more effort, concentrate better and avoid inattentiveness. Maybe even their arousal increases. Increasing slow potential amplitudes might reflect an increase of any of these task-general processes. Secondly, the investment of more effort should lead to better memory performance. Participants might indeed *maintain* more information in visual WM under incentives as compared to the baseline condition. Slow potentials should additionally reflect the enhanced maintenance processes. The maintenance of more feature information should be observable especially for higher set sizes, that is set sizes around and above visual WM capacity limit (set sizes above three). This should be observable in form of a boost of K_{max} and a boost of the EKP amplitudes for these higher set sizes. Contrary, as lower set sizes are well below participants' visual WM capacity, participants probably already hold all relevant feature information in the baseline condition and can consequently not hold more information in the incentive condition. To have the ability to observe potential improvements in visual WM capacity through incentives we included conditions with above-capacity set sizes into the present experiment. We ran conditions up to six objects because Luck (as cited in Cowan, 2001) reports of one participant trained in remembering colored objects, who was able to remember up to six colors.

As already outlined in Chapter 4, Vogel and colleagues (Vogel & Machizawa, 2004; McCollough, et al., 2007) discuss that the utmost advantage of the CDA is that it specifically reflects the process of visual WM maintenance. All other task-general processes, such as processes of perception, effort or arousal, are subtracted out. The posterior slow potentials, in contrast, are discussed as being not specific to this single process, but might additionally reflect several of these task-general processes (Vogel & Machizawa, 2004; McCollough et al., 2007). Crucially, Vogel and colleagues (McCollough et al., 2007) argue that these task-general effects should emerge bilaterally, that means equally for contralateral as well as ipsilateral slow potentials. Therefore, we hypothesize that the investment of more effort and concentration on the task should be reflected in a higher amplitude for contralateral as well as ipsilateral slow potentials under incentives as compared to the baseline condition. Furthermore, additional improvements in maintenance processes proper should be reflected in the CDA. As already outlined above, remembering more features due to improved maintenance processes should be observable mainly for higher set sizes. Actually, the same effect as in the CDA should also be evident in underlying contralateral slow potentials. Please note that observing bilateral incentive effects in the slow potentials does not exclude an additional effect in the contralateral slow potentials due to improved maintenance processes.

Furthermore, in line with the reasoning of Vogel and Machizawa (2004; see Chapter 4.2), we expect that behavioral measures of visual WM capacity (K_{max}) would predict the asymptote of the CDA in both conditions. CDA should reach an asymptote (a) for smaller set sizes for participants with poor visual WM capacity and (b) for higher set sizes for participants with high visual WM capacity. This relation should be reflected in a correlation between K_{max} and the CDA amplitude difference between set size three and four. A similar relation might or might not emerge for posterior slow potentials and would be informative concerning their interpretation.

In order to gain an undistorted baseline for visual WM performance, the baseline condition has to be measured first, when participants are not yet aware of the incentive manipulation. Taking the risk of confounding incentive effects with practice effects, we therefore decided to run the baseline condition always before the incentive condition. Crucially, we informed participants only after the first block about reward for good performance in the second block. However, practice should lead to continuous performance improvements, whereas the experimental manipulation should result in a sudden rise in performance from Block 1 to Block 2. In order to assure that our effects mirror incentive effects and not mere practice effects, we therefore tested for this sudden rise.

5.2 Methods

5.2.1 Participants

Sixteen students of Saarland University (1 left-handed, mean age: 25.53 years, range: 22-30 years, 10 female) participated in this experiment. All participants had normal or corrected-to-normal vision. One participant had to be excluded from further analysis because of excessive EEG artifacts. For the first session, the baseline condition, participants received 8 € per hour for participation. The amount of additional payment participants received for the incentive condition depended on their individual performance as detailed below. All participants gave informed consent after the nature of the study had been explained to them.

5.2.2 Stimuli

Stimuli were seven colored squares (red, blue, green, yellow, black, white, purple) with a size of 0.65° x 0.65° which were presented against a gray background. The stimuli appeared in two rectangular regions (4° × 7.3° each) that were centered 3° to the right and to the left of the center of the screen.

5.2.3 Design and procedure

Participants performed two blocks of a lateralized change detection task (see Figure 5.1) with a short brake in between. Both blocks were exactly the same, except that in the second block participants were paid according to their performance. The design of the lateralized change detection task was as follow: Before the presentation of the memory array, an arrow was presented for 200 ms. This arrow indicated which of the two hemifields was relevant and consequently had to be remembered. In 50% of the trials, the arrow pointed to the left, in the remaining 50% of the trials it pointed to the right. Between the presentation of the arrow and the memory array a blank screen (only containing the fixation cross) was presented jittered randomly between 100-200 ms to prevent a systematic timing between processing the arrow and processing the memory array. The memory array was presented for 100 ms and consisted of two rectangular regions, one in each hemifield. In each of these regions, two to six colored squares were presented. Within the rectangular regions, item positions were set at random with the limitation that the minimal distance between the centers of each pair of items was at least 2°. Within one trial, colors were randomly chosen with the constraint that a specific color could appear only once within one hemifield. Participants were instructed that the best method to encode the stimuli was to fixate on the central fixation cross and covertly move their attention to the side indicated by the arrow. The retention interval lasted 900 ms. In 50% of the trials one of the squares in the relevant hemifield changed its color from memory to test array, in the other half of trials all colors remained the same. Participants had to press one key to indicate a color change and another key when no color had changed. The assignment of keys to response class was counterbalanced across participants. The test array lasted 2000 ms longest, but was terminated with participants' key press. Participants were seated at a distance of 70 cm from the monitor. In each block we ran 100 trials per set size. This resulted in a total of 1000 trials, 500 trials per block.

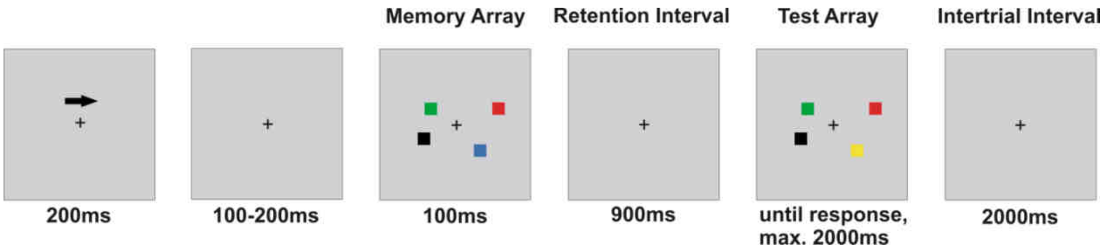

Figure 5.1. Schematic illustration of the task procedure of Experiment 1

The first block served as baseline condition for visual WM performance and associated electrophysiological correlates. In the short break between the first and the second block (the incentive condition) participants were informed that in the second block they would earn money dependent on their performance accuracy. We told them that, additionally to the already earned money in the first block, they have the chance to gain maximally further 15 € in the second block. This constitutes an additional performance-dependent payment of up to 0.75 times the basis payment.

We calculated K_{max} as described in Chapter 2.3.

5.2.4 EEG recording and analysis

The experiment was run in a sound- and electromagnetically shielded chamber. EEG activity was recorded continuously from 63 Ag/AgCl electrodes (Easy Cap, Falk Minow Services, Germany) arranged according to the extended international 10-20 system. Impedances were kept below at least 10kΩ for EOG-electrodes and 5kΩ for the other electrodes. Signals were amplified with an AC coupled amplifier (Brain Amps, Brain Products, Munich), sampling rate was 500 Hz with a 250 Hz analog low-pass filter and a time constant of 10 s. A left mastoid reference was used during recording and signals were re-referenced offline to the averaged mastoids. Vertical and horizontal ocular artifacts were monitored by four ocular electrodes (above and below the right eye and at the outer canthi of both eyes) and corrected according to Gratton, Coles and Donchin (1983). If the number of blinks was small, no correction was applied but the blink-contaminated trials were excluded.

ERPs were extracted by stimulus-locked signal averaging from -200 to 1000 ms relative to the onset of the memory array for each number of items-condition, separately for each Block. Data were baseline-corrected with respect to the 200 ms pre-stimulus interval and digitally low pass filtered at 20 Hz. Epochs containing artifacts were excluded from further analysis. Analysis was based only on trials with correct responses. Data were averaged over matches and mismatches, because we were interested in the retention interval, a period in which these two types of trials are not yet discriminable for the subjects and so processing is the same.

We calculated contralateral and ipsilateral slow potentials as well as the CDA for parietal and occipital electrode sites. We calculated contralateral slow potentials for each electrode by averaging activity over right (left) electrodes when the relevant stimuli were presented in the left (right) hemifield. We calculated ipsilateral slow potentials equivalently by averaging activity over right (left) electrodes when the relevant stimuli were presented in the right (left) hemifield. To obtain the CDA we calculated the difference waves between contralateral and ipsilateral activity with regard to the attended hemifield. Consequently, we differentiated electrodes with respect to the relevant hemifield and not with respect to hemispheres. Therefore, in the following, we refer to electrode positions contralateral and ipsilateral CP1/2, CP3/4, CP5/6, TP7/8, P1/2, P3/4, P5/6, P7/8, PO3/4, PO7/8 and O1/2.

5.3 Results

Data were analyzed by analysis of variance (ANOVA) or *t*-tests. If the ANOVA-results were corrected for non-sphericity using the Greenhouse-Geisser-correction (Greenhouse & Geisser, 1959), we report Greenhouse-Geisser epsilons (ε) and corrected *p*-values (p_{corr}) together with the original *F*-values and original degrees of freedom. Effects and interactions were further decomposed by contrasts.

In all graphs, 95%-confidence intervals are calculated according to the procedure described by Jarmasz and Hollands (2009) and are based on the error term of the respective effect of interest. We corrected the critical effects' *df*s appropriately if εs were too low, as suggested by Loftus and Masson (1994). The effects on which the confidence intervals are based can be found below each figure.

5.3.1 Behavioral data

Mean response accuracies as a function of block (baseline vs. incentive condition) and number of items (2, 3, 4, 5, or 6 items) are given in Table 5.1. A 2 (block) × 5 (number of items)-ANOVA on response accuracies yielded the following results: A significant effect of the number of items, $F(4,56) = 91.70$, $\varepsilon = .55$, $p_{\mathrm{corr}} < .001$, $\eta^2_{\mathrm{partial}} = .87$, which reflects the expected decrease in accuracy with increasing number of items, all pairwise comparisons were significant, all Fs > 11.43, all ps < .01. Additionally, there was a significant effect of block, $F(1,14) = 36.39$, $p < .001$, $\eta^2_{\mathrm{partial}} = .72$, For each set size, participants performed better in the block with incentives, all Fs > 6.79, all ps < .05. There was no interaction, $F(4,56) = 0.63$, $\varepsilon = .70$, $p_{\mathrm{corr}} = .59$, $\eta^2_{\mathrm{partial}} = .04$.

Table 5.1

Mean Response Accuracies as a Function of Block and Number of Items

	Number of items				
Block	2	3	4	5	6
Baseline condition	.965	.936	.865	.803	.760
Incentive condition	.983	.959	.905	.835	.797

There was a significant increase in K_{max} from Block 1 (mean = 3.32) to Block 2 (mean = 3.82), $t(14) = 3.52$, $p < .01$.

To determine whether the observed effect of block (baseline condition vs. incentive condition) is really an incentive effect and not just a practice effect, we conducted the following testing: We separated each block in sub-blocks of 100 trials and ran an ANOVA on the last two sub-blocks of the baseline condition (Block 1) and the first sub-block of the incentive condition (Block 2). Practice effects should lead to an equal and steady performance improvement from the second to last sub-block of Block 1 to the last sub-block of Block 1 to the first sub-block of Block 2. However, an incentive effect should lead to the following result pattern: The last two sub-blocks of Block 1 should not differ in response accuracies, whereas the accuracies of the first sub-block of Block 2 should be significantly higher than those of the last sub-block of Block 1.

As predicted, the last two sub-blocks of the baseline condition did not differ in overall accuracies, $t(14) = 0.57$, $p = .58$, whereas the last sub-block of the baseline condition and the first sub-block of the incentive condition differed in the predicted direction, $t(14) = 2.46$, $p < .05$. This data pattern clearly indicates that the block effect on mean accuracies goes back to the predicted incentive-effects and speaks against an interpretation in terms of practice effects.

5.3.2 Electrophysiological data

As anticipated, the number of relevant items had the strongest effect on activity measured over electrodes at posterior recording sites, especially at P3/4, P5/6, P7/8, PO3/4 and PO7/8. We consequently pooled over these five electrode sites. Effects on CDA amplitudes were analyzed by an ANOVA on the number of items (2, 3, 4, 5, or 6) and block (baseline condition vs. incentive condition); effects on slow potential amplitudes were analyzed by an ANOVA on the number of items, block and hemisphere (contralateral vs. ipsilateral hemisphere with respect to the relevant hemifield). Both electrophysiological analyses were based on mean voltage amplitudes averaged over the time window from 350 to 700 ms after onset of the memory array.

First aim of the study: Replication of the CDA and examination of slow potential patterns in the baseline condition

A 5 (number of items)-ANOVA on CDA amplitude in Block 1 yielded a significant main effect, $F(4,56) = 8.81$, $\varepsilon = .78$, $p_{\text{corr}} < .001$, $\eta^2_{\text{partial}} = .39$, that goes back to a difference between set sizes two and three, $F(1,14) = 28.54$, $p < .001$. CDA amplitude did not differ for the remaining set sizes, all Fs < 1.98, all $ps > .18$. (see left side of Figure 5.2). This result constitutes the desired replication of the data of Vogel and Machizawa (2004).

As can be seen in Figure 5.3, the number of items affected contralateral as well as ipsilateral slow potential amplitudes, whereby the load effect was more pronounced for contralateral slow potentials. A 2 (hemisphere) × 5 (number of items)-ANOVA on slow potential amplitudes in Block 1 yielded a significant effect of hemisphere, $F(1,14) = 6.74$, $p < .05$, $\eta^2_{\text{partial}} = .33$, a significant effect of the number items, $F(4,56) = 17.95$, $\varepsilon = .50$, $p_{\text{corr}} < .001$, $\eta^2_{\text{partial}} = .56$, and a significant interaction, $F(4,56) = 8.81$, $\varepsilon = .78$, $p_{\text{corr}} < .001$, $\eta^2_{\text{partial}} = .39$ (see Figure 5.4). Contralateral and ipsilateral slow potential amplitudes did not differ for set size two, $p = .53$, but for all remaining set sizes, all Fs > 6.93, all ps < .05. Contralateral slow potentials' amplitude significantly increased from set sizes two to five, whereby all pairwise contrasts were significant, all Fs > 5.31, all ps < .05. There was no amplitude difference for set sizes five and six, $F(1,14) = 1.07$, $p = .32$. For the ipsilateral slow potentials, there was a significant increase in amplitude from set sizes two to four, both Fs > 4.60, both ps < .05; set sizes four and five differed marginally, $F(1,14) = 3.03$, $p = .10$, whereas there was no amplitude difference for set sizes five and six, $F(1,14) = 0.71$, $p = .41$. In sum, there were load effects for contralateral as well as ipsilateral slow potential amplitudes.

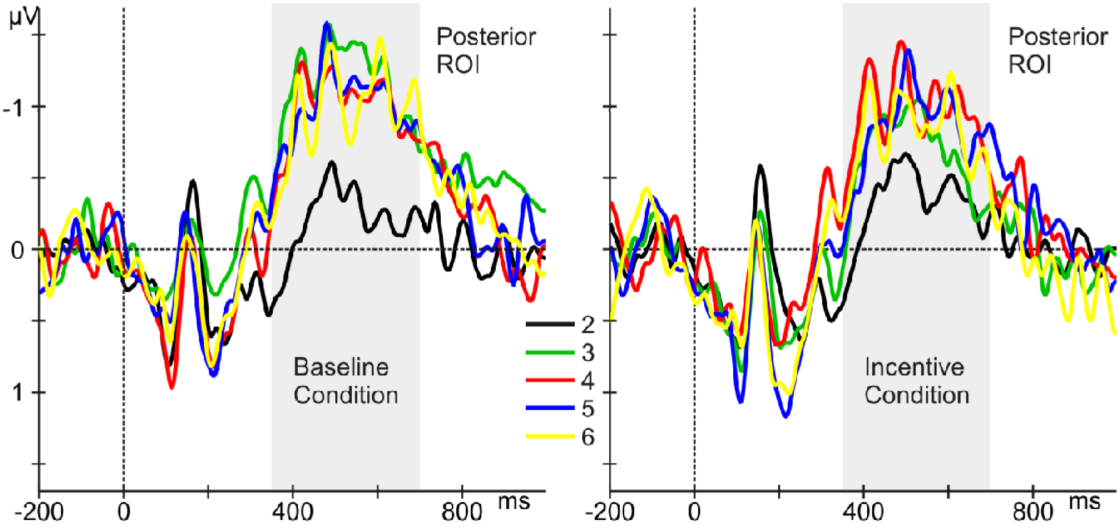

Figure 5.2. Grand averaged CDA relative to the onset of the memory array at posterior ROI (P3/4, P5/6, P7/8, PO3/4, PO7/8). Colors code the number of items. The baseline condition is shown on the left, the incentive condition on the right.

As can be seen in Figure 5.3, there is a posterior positivity starting at about 200 ms over contralateral as well as ipsilateral recording sites, preceding the slow potentials. This posterior positivity shows load-dependent modulations up to set size 4 where it reaches an asymptote. An exploratory 5 (number of items) × 2 (hemisphere)-ANOVA on the amplitudes of this posterior positivity in Block 1 in the time window from 200-260 ms after onset of the memory array confirmed a significant effect of the number of items, $F(4,56) = 14.71$, $\varepsilon = .43$, $p_{corr} < .001$, $\eta^2_{partial} = .51$. Neither the effect of hemisphere nor the interaction was significant, $F(1,14) = 2.60$, $p = .13$, $\eta^2_{partial} = .16$, and $F(4,56) = 1.72$, $\varepsilon = .59$, $p_{corr} = .19$, $\eta^2_{partial} = .11$, respectively. Amplitudes increased with load up to set size four, both *F*s > 12.79, both *p*s < .01, but did not differ between four, five and six items, all *F*s < 1.65, all *p*s > .21.

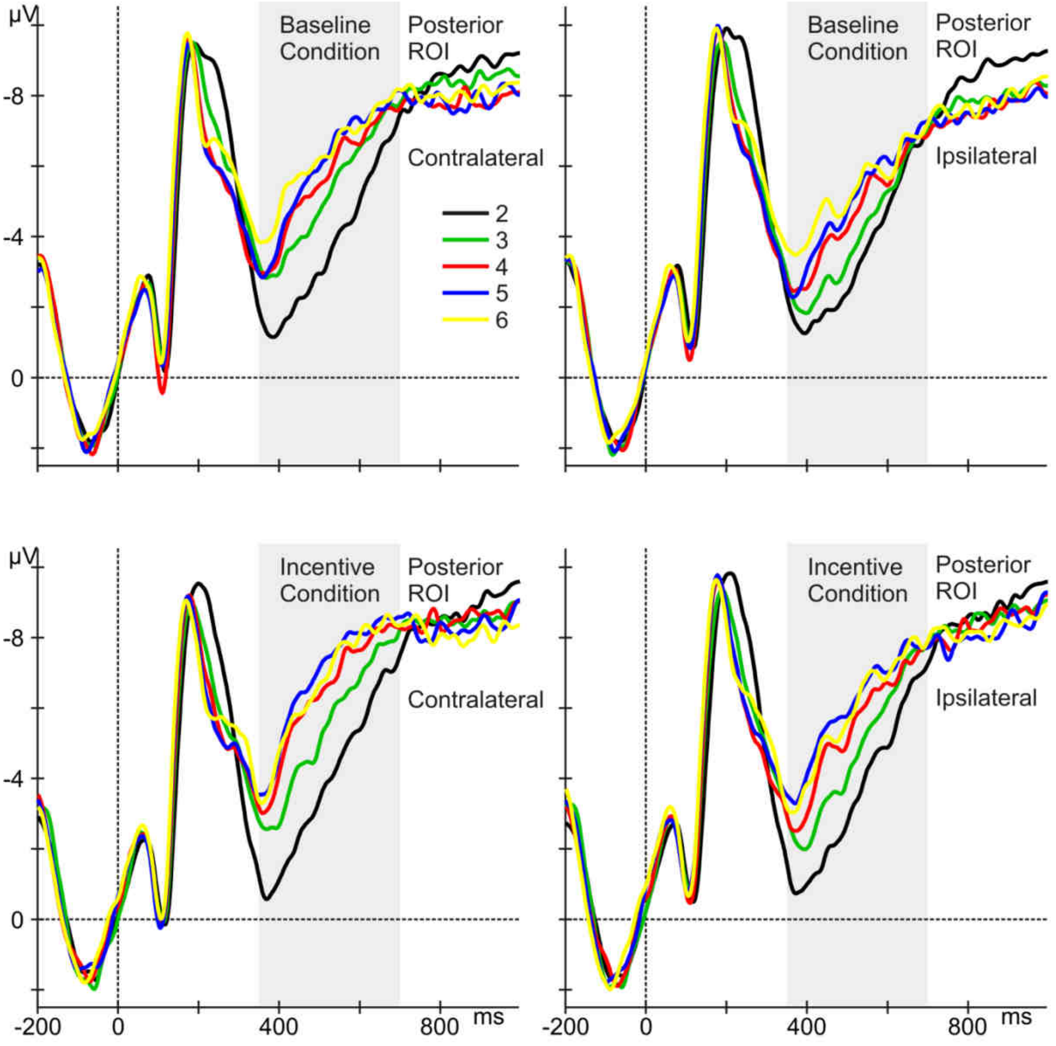

Figure 5.3. Grand averaged contralateral (left) and ipsilateral (right) slow potentials relative to the onset of the memory array at the posterior ROI (P3/4, P5/6, P7/8, PO3/4, PO7/8). Colors code the number of items. The baseline condition is shown in the upper and the incentive condition in the lower part of the figure.

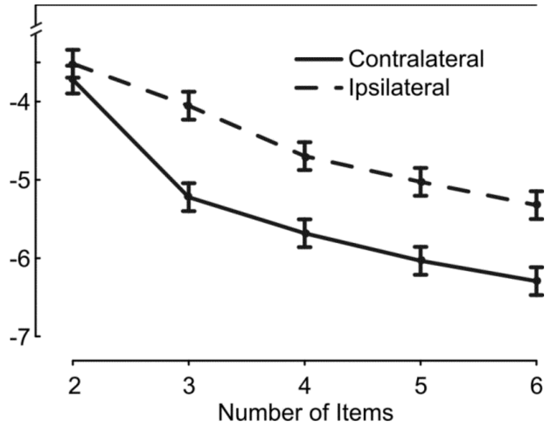

Figure 5.4. Contralateral and ipsilateral slow potentials as a function of the number of items in Block 1. The displayed 95%-confidence intervals are based on the hemisphere × number of items-interaction.

Second aim of the study: Incentive effects

The slow potentials as a function of the number of items, block and hemisphere are shown in Figure 5.3. As can be seen in Figure 5.5, there is an effect of block; contralateral and ipsilateral slow potential amplitudes are higher in the incentive condition as compared to the baseline condition. This block effect is strongest for three and four items. A 5 (number of items) × 2 (block) × 2 (hemisphere)-ANOVA on mean slow potential amplitudes revealed a significant effect of number of items, $F(4,56) = 30.36$, $\varepsilon = .43$, $p_{corr} < .001$, $\eta^2_{partial} = .68$, a significant effect of block, $F(1,14) = 5.61$, $p < .05$, $\eta^2_{partial} = .29$, a significant effect of hemisphere, $F(1,14) = 6.05$, $p < .05$, $\eta^2_{partial} = .30$, and a significant interaction between hemisphere and number of items, $F(4,56) = 9.97$, $\varepsilon = .58$, $p_{corr} < .001$, $\eta^2_{partial} = .42$. The three-way interaction was not significant, $F(4,56) = 1.62$, $\varepsilon = .61$, $p_{corr} = .21$, $\eta^2_{partial} = .10$. The main effect of number of items as well as the interaction between hemisphere and number of items are already reported above for Block 1 only and did not considerably change when analyzing data from both blocks. We consequently do not report them again. Concerning the block effect, there was no increase from Block 1 to Block 2 in slow potentials' amplitude for set size two, $F(1,14) = 0.21$, $p = .65$, a marginally significant increase for set size three, $F(1,14) = 2.43$, $p = .14$, a significant increase for set size four and five, $F(1,14) = 4.59$, $p = .05$ and $F(1,14) = 13.24$, $p < .01$, respectively, and a marginally significant increase for set size six, $F(1,14) = 2.24$, $p = .16$. This result pattern explains the marginally significant interaction between block and number of items, $F(4,56) = 2.07$, $\varepsilon = .81$, $p_{corr} = .11$, $\eta^2_{partial} = .13$. In sum, slow potential amplitude significantly increased from Block 1 to Block 2 for set sizes four and five, indicating the hypothesized incentive effect at set sizes around capacity limits.

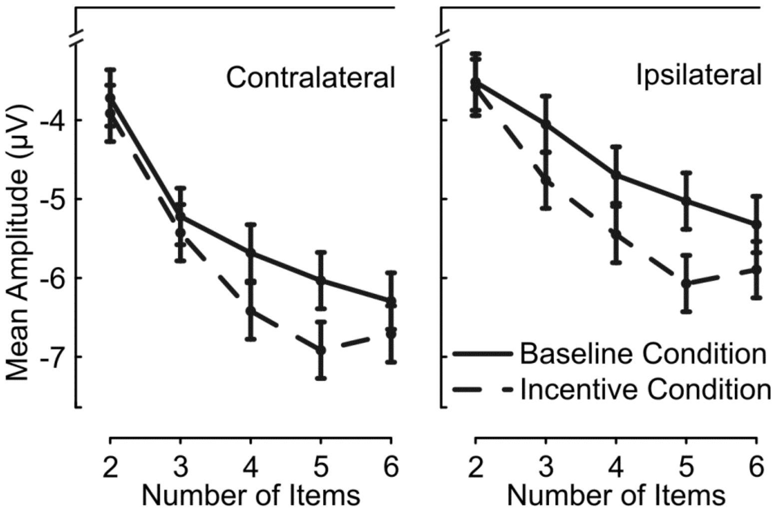

Figure 5.5. Contralateral and ipsilateral slow potentials as a function of block and the number of items. The displayed 95%-confidence intervals are based on the main effect of block.

That the session effect is equally pronounced for contralateral as well as ipsilateral slow potentials explains why there is no session effect in the CDA. A 5 (number of items) × 2 (block)-ANOVA on mean CDA amplitudes yielded a significant main effect of number of items, $F(4,56) = 9.97$, $\varepsilon = .58$, $p_{\text{corr}} < .001$, $\eta^2_{\text{partial}} = .42$, but no effect of block, $F(1,14) = 1.01$, $p = .33$, $\eta^2_{\text{partial}} = .07$, and no interaction between number of items and block, $F(4,56) = 1.62$, $\varepsilon = .61$, $p_{\text{corr}} = .21$, $\eta^2_{\text{partial}} = .10$ (see Figures 5.2 and 5.6). Crucially, the incentive effect observed in the behavioral data was not mirrored by an incentive effect on CDA amplitudes. The effect of the number of items is already reported above for Block 1 only and goes back to a significant increase in amplitude between two and three items only, $F(1,14) = 3.58$, $p < .001$; for all other numbers of items, all Fs < 0.50, all ps > .49.

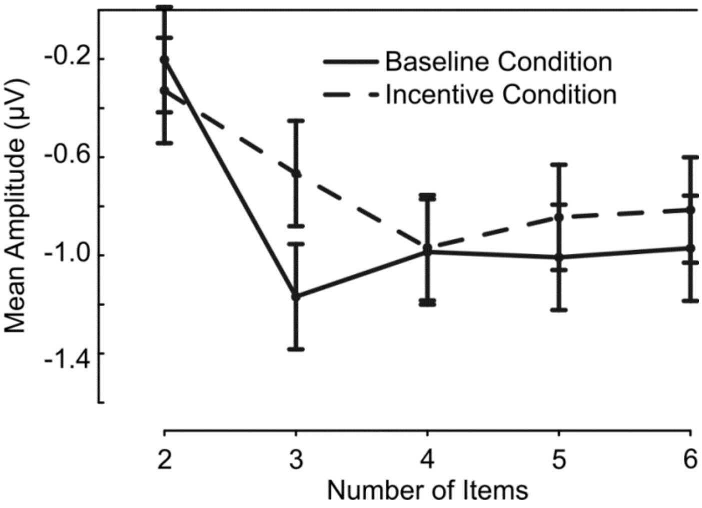

Figure 5.6. CDA as a function of block and number of items. The displayed 95%-confidence intervals are based on the main effect of block.

In the baseline condition, we found no correlation between K_{max} and the increase in amplitude from three to four items for either CDA or slow potentials, all rs < .32, all ps > 24. In the incentive condition, in contrast, there was a significant correlation between K_{max} and the increase from three to four items in contralateral as well as ipsilateral slow potential amplitudes, $r = .65$, $p < .01$, $r = .57$, $p < .05$, respectively, but not for the CDA, $r = .03$, $p = .92$.

5.4 Discussion

One main aim of this study was to evaluate the lateralized change detection design and the associated electrophysiological components—posterior slow potentials and CDA—with respect to their suitability for the dissertation project. We aimed to replicate a CDA, whose amplitude is sensitive to manipulations of visual WM load. We were also interested in the behavior of posterior slow potential activity, as they constitute the building block of the CDA.

Indeed, we observed a CDA with amplitude modulations as a function of the number of items within limits of behavioral K_{max}. The amplitude of the CDA reached its asymptote at set size three, that is close to mean K_{max} (mean $K_{\text{max}} = 3.3$). This result is in line with the data of Vogel & Machizawa (2004), where the CDA amplitude also increased up to set size three, where it reached its asymptote. Furthermore, amplitudes of contralateral as well as ipsilateral posterior slow potentials were sensitive to memory load, whereby the load effect was more pronounced for contralateral slow potentials as compared to their ipsilateral counterparts.

In an exploratory analysis on a posterior positivity starting about 200 ms after onset of memory array we made a serendipitous observation. The amplitude of the posterior positivity was a function of set size until it reached an asymptote for four items. The observed asymptotic trend in amplitude for more than four items is in line with observations that humans can hold only four items at once in the focus of attention (cf., Cowan, 2001; Pylyshyn, 2001; Scholl, 2009). Maybe this component reflects attentional allocation towards the items that might underlie the creation of object-files for the presented items for their subsequent maintenance in visual WM. An analysis on the training data in Chapter 13 will shed further light on this component and we will therefore continue the discussion there.

Our second aim was to investigate the plasticity of visual working memory efficiency via an incentive manipulation. The two related questions were firstly, if visual WM in general and the lateralized change detection design in particular is sensitive to an incentive manipulation. As already reported above, there are inconsistencies across experiments as to whether reward anticipation can improve WM functioning. And secondly, we wanted to figure out if possible behavioral improvements are reflected in the components of interest, the posterior slow potentials and the CDA.

Participants' mean response accuracies increased under incentives as compared to the baseline condition. Furthermore, mean K_{max}, the mean capacity limit of our participants, increased in the incentive condition, indicating that participants maintained more feature information as compared to the baseline condition. As predicted, we observed a sudden performance improvement from Block 1 (the baseline condition) to Block 2 (the incentive condition), but not within a comparable interval within Block 1. This data pattern confirms clear incentive effects, as practice effects should show up smoother.

This increased memory performance was hypothesized to be reflected in the CDA. Remarkably, CDA amplitude did not increase under incentives. What can we conclude from this result pattern? Participants were able to hold in memory significantly more information but without a respective increase in CDA amplitudes. A look on the amplitude pattern of contralateral and ipsilateral slow potentials explains the missing incentive effect in the CDA. Incentive effects emerge completely bilateral, equally pronounced for the contralateral as well as ipsilateral slow potentials, and hence are completely subtracted out for CDA amplitudes.

Let us have a closer look on the incentive effects in the slow potentials. As slow potentials mirror cognitive effort (Rösler et al., 1997) and effort should increase under incentives, we predicted that slow potential amplitude should increase. This is exactly what we observed. However, in the introduction, we discussed two possible processes that might be reflected by the slow potentials. Firstly, participants might have better concentrated on the task and avoided inattentiveness. These effort effects should show up bilaterally. Secondly, participants might maintain more feature information under incentives. Vogel and colleagues (e.g., McCollough et al., 2007; Vogel & Machizawa, 2004) showed that maintenance processes emerge—at least in part—lateralized in the lateralized change detection task. Therefore, an increase in maintained feature information was hypothesized to show up lateralized; it should be more pronounced in contralateral slow potentials as compared to ipsilateral slow potentials (and should hence emerge in the CDA) However, as discussed, we observed an equally pronounced incentive effect for contralateral as well as ipsilateral slow potentials. Does consequently the incentive effect in the slow potentials only mirror increased task-general processes as effort and not maintenance processes? We do not believe so. We observed an increase in K_{max}, indicating that more item information is retained under incentives. We hypothesized that maintenance should be boosted especially for set sizes around capacity limit, that means for these set sizes more feature information should be held in visual WM. Interestingly, incentive effects in the slow potentials were restricted to set sizes four and five, exactly those set sizes for which we expected incentive effects to mirror truly increased maintenance processes. This constitutes suggestive evidence for the assumption that this effect is not only due to increased effort or arousal but might mirror WM maintenance processes.

Furthermore, bilateral slow potential amplitudes are sensitive to individual capacity limitations in the incentive condition. Under incentives, participants with higher memory capacity had a higher increase in amplitude from set size three to four, indicating that they have a larger amount of cognitive resources left for the processing of four items as compared to low capacity participants. This is reflected in a correlation between the increase in contralateral as well as ipsilateral slow potential amplitudes from three to four items and K_{max}. This correlation constitutes a further indication for the strong coupling of slow potential activity and visual WM performance under incentives.

To sum up, participants perform better under incentives and increase their K_{max}; that means they increase the amount of maintained information. This effect is mirrored in bilateral slow potential amplitude. Although we cannot clearly dissociate effort processes from maintenance processes, the slow potentials mirror processes that go hand in hand with a better visual WM capacity under incentives. Contrary, the CDA is not sensitive for these improvements in visual WM maintenance.

We can conclude that the paradigm is well suited as a tool for mirroring plasticity in visual WM. In contrast to the CDA, the slow potentials mirrored plasticity effects. Therefore, we argue that additionally to the CDA, the slow potentials constitute a valuable measure of visual WM maintenance processes and should not only be considered a building block of the CDA. They might be the more sensitive measure for plasticity effects of visual WM functioning.

6 Experiment 2: What does Ipsilateral Delay Activity Reflect? Inferences from Slow Potentials in a Lateralized Visual Working Memory Task[1]

6.1 Introduction

Experiment 1 delivered several indications that maintenance activity in the lateralized change detection task might—at least in parts—emerge bilaterally. In other words, ipsilateral delay activity might also mirror maintenance processes. This would challenge the logic of the contralateral control method (see Chapter 3) that is employed to extract the CDA. According to this logic, ipsilateral delay activity reflects only task-general processes; the process of interest—the maintenance process—in contrast, is purportedly reflected only by the contralateral delay activity.

In line with the load-dependent ipsilateral delay activity in Experiment 1, other researchers also reported load-dependent ipsilateral delay activity in the retention period of a lateralized change detection task (Robitaille et al., 2009). Because the observed bilateral activity is disguised when only the CDA is considered, Robitaille et al. (2009) caution not simply to use the ipsilateral activity as a means to control for unspecific contralateral activity. They assume that both lateralized activity and bilateral activity are related to the process of maintaining information in visual WM. As the standard lateralized change detection

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[1] This chapter is an adapted version of Arend and Zimmer (2011). Copyright © 2012 by The MIT Press. Adapted with permission.

paradigm was employed, the number of items in the relevant hemifield was always identical to the number of items in the irrelevant hemifield, that is, their numbers were perfectly correlated. Therefore, it cannot be decided whether ipsilateral neural activity that covaries with memory load is caused by the relevant or irrelevant items. We now describe the two possible explanations in detail.

One possibility is that the relevant items might be processed bilaterally due to advantages that might arise from processing information in both hemispheres over processing in only one hemisphere. Umemoto, Drew, Ester and Awh (2010) reported a *bilateral advantage* effect for storage of information in visual WM. If the visual input was provided in both hemifields, participants' visual WM performance was found to be better than if the same visual input was presented unilaterally. In the lateralized change detection design, to use both hemispheres, that is, to transfer the information from the contralateral to the ipsilateral hemisphere, might also improve the processing of the relevant items. Gratton and colleagues (Gratton, Corballis & Jain, 1997; Shin, Fabiani & Gratton, 2006) examined the hemispheric organization of visual memory. Similar to the lateralized change detection task, stimuli were initially presented lateralized. Critically, however, the test array was presented centrally. Despite the central presentation of the test array, the amplitude difference between old and new items of ERPs measured during the test interval were larger over the hemisphere contralateral to the hemifield of initial encoding as compared to the ipsilateral hemisphere. This finding indicates that information was stored in both hemispheres, but with a contralateral bias. These distinct yet converging lines of research indicate that bilateral processing of to be remembered information might in some cases be beneficial for task performance.

The second possibility is that, irrelevant items which the underlying neural network received as perceptual input might cause neural activity over the hemisphere ipsilateral to the relevant hemifield. It is well established that under some conditions irrelevant, to be ignored stimuli are processed to a certain extent (Erikson & Erikson, 1974), even when they are presented rather far away from the relevant stimuli (Gatti & Egeth, 1978). However, in line with the well examined selective attention effect in perception (e.g., Moran & Desimone, 1985; Hopfinger, Luck & Hillyard, 2004; Hillyard, Vogel & Luck, 1998), attention might amplify processing of the relevant items. Allocation of attention towards a certain location might increase the number of neurons that process the stimuli at that location (Bundesen, Habekost & Kyllingsbaek, 2005). This might lead to both, an enhancement in processing and a higher cortical activation level. Concerning the lateralized change detection paradigm, the contralateral slow potentials should show a higher load dependent activation level than the ipsilateral slow potentials.

As previously mentioned, within the lateralized change detection task, it is impossible to unravel the effects of the amount of items presented in the relevant and the irrelevant hemifield, because their numbers are typically identical. We orthogonally varied the number of items in both hemifields, in order to examine the effect of the number of relevant items independently of the effect of the number of irrelevant items and vice versa. This allows us to determine how processing of the relevant and the irrelevant items influences the amplitudes of slow potentials over the contralateral and ipsilateral hemisphere, respectively.

Slow potentials contralateral to the relevant hemifield should increase with the number of relevant items, because these slow potentials are supposed to reflect the maintenance of items in visual WM. This prediction is in line with earlier research on the lateralized change detection task, as reviewed above (Klaver et al., 1999; Vogel & Machizawa, 2004, Robitaille et al., 2009). In comparison to contralateral slow potentials, the behavior of slow potentials ipsilateral to the relevant hemifield is less well understood.

(1) If irrelevant items are completely filtered out and relevant items are only processed laterally, the slow potentials over the hemisphere ipsilateral to the relevant hemifield are neither influenced by the relevant nor the irrelevant items, and their amplitude should be of equal size in all conditions.

(2) Alternatively, relevant items might be processed bilaterally. In this case, both the amplitudes of the contralateral and ipsilateral slow potentials would be a function of the number of relevant items. However, the contralateral hemisphere receives the visual input first and might therefore hold a more distinct or enhanced representation. As a consequence, the number of relevant items might influence the amplitude of slow potentials over the contralateral hemisphere more strongly than over the ipsilateral one.

According to hypotheses (1) and (2) irrelevant items are completely filtered out of visual WM meaning that the number of irrelevant items should not influence the amplitude of the slow potentials.

(3) If irrelevant items are not filtered out but processed to a certain degree, the amplitude of slow potentials over the hemisphere ipsilateral to the relevant hemifield should increase with the number of irrelevant items. However, because attention is focused on the relevant hemifield, processing of relevant items should be enhanced and therefore cause a stronger amplitude modulation in slow potentials measured over the contralateral hemisphere than processing of irrelevant items causes in slow potentials over the ipsilateral hemisphere.

In all three activation patterns as described above, the amplitude modulations of the slow potentials ipsilateral to the relevant hemifield are either weaker than those of the contralateral slow potentials or even absent. In all cases, therefore, subtracting ipsilateral from contralateral slow potentials always results in a negative-going difference wave (the CDA), the amplitude of which is a function of the number of relevant items. However, the three hypotheses lead to different implications concerning the interpretation of the CDA. (1) If only contralateral effects of the number of relevant items are observed, the CDA is influenced only by processing of relevant items. (2) If ipsilateral effects of the number of relevant items are also observed, the CDA reflects the degree of lateralization of processing of relevant items. (3) In the case that the ipsilateral potentials show effects due to processing of the irrelevant items, the CDA reflects the amount of processing bias towards the attended hemifield. Crucially, the CDA does not differentiate between these three predictions. However we can test these assumptions against each other by analyzing contralateral and ipsilateral slow potentials.

6.2 Methods

6.2.1 Participants

Sixteen students of Saarland University (one left-handed, mean age: 22.4 years, range: 20-25, 8 female) participated in this experiment. All participants had normal or corrected-to-normal vision. One participant had to be excluded from further analysis because of excessive EEG artifacts. Participants were paid 8€ per hour of participation.

6.2.2 Stimuli

Stimuli were seven colored squares (red, blue, green, yellow, black, white, purple) with a size of 0.65° x 0.65° and were presented against a gray background. The stimuli appeared in two rectangular regions (4° × 7.3° each) that were centered 3° to the right and to the left of the center of the screen.

6.2.3 Design and procedure

Participants performed a lateralized change detection task (see Figure 6.1). Before the presentation of the memory array, an arrow was presented for 200 ms. This arrow indicated which of the two hemifields was relevant and consequently had to be remembered. In 50% of the trials, the arrow pointed to the left, in the remaining 50% of the trials it pointed to the right. Between the presentation of the arrow and the memory array a blank screen (only containing the fixation cross) was presented for 100-200 ms (randomly) to prevent a systematic timing between processing the arrow and processing the memory array. The memory array was presented for 100 ms and consisted of two rectangular regions, one in each hemifield. In each of these regions, one to three colored squares were presented. Participants were instructed that the best method to encode the stimuli was to fixate on the central fixation cross and covertly move their attention to the side indicated by the arrow. The retention interval lasted 900 ms. In 50% of the trials one of the squares in the relevant hemifield changed its color from memory to test array, in the other half of trials all colors remained the same. Participants had to press one key to indicate a color change and another key when no color had changed. The assignment of keys to response class was counterbalanced across participants. The test array lasted 2000 ms longest, but was terminated with participants' key press. The number of relevant, to be remembered, items and the number of irrelevant items were varied orthogonally between one and three. This resulted in 900 trials, 100 for each number of relevant × number of irrelevant items-condition.

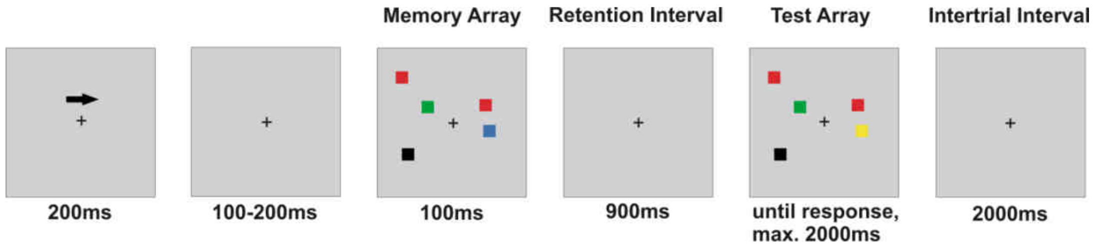

Figure 6.1. Schematic illustration of the task procedure in Experiment 2.

Within the rectangular regions, item positions were set at random with the limitation that the minimal distance between the centers of each pair of items was at least 2°. Within one trial, colors were randomly chosen with the constraint that a specific color could appear only once within one hemifield. Participants were seated at a distance of 70 cm from the monitor.

6.2.4 EEG recording and analysis

The experiment was run in a sound- and electromagnetically shielded chamber. EEG activity was recorded continuously from 28 Ag/AgCl electrodes (Easy Cap, Falk Minow Services, Germany) arranged according to the extended international 10-20 system. We recorded at parietal and occipital electrode sites: CPz, CP2, CP4, CP6, TP8, Pz, P2, P4, P6, P8, POz, PO4, PO8, Oz, O2 (and left sides respectively). Impedances were kept below at least 10kΩ for EOG-electrodes and 5kΩ for the other electrodes. Signals were amplified with an AC coupled amplifier (Brain Amps, Brain Products, Munich), sampling rate was 1000 Hz with a 250 Hz analog low-pass filter and a time constant of 10 s. A left mastoid reference was used during recording and signals were re-referenced offline to the averaged mastoids. Vertical and horizontal ocular artifacts were monitored by four ocular electrodes (above and below the right eye and at the outer canthi of both eyes) and corrected according to Gratton, Coles and Donchin (1983). If the number of blinks was small, no correction was applied but the blink-contaminated trials were excluded.

ERPs were extracted by stimulus-locked signal averaging from -200 to 1000 ms relative to the onset of the memory array for each number of relevant items × number of irrelevant items-cell. Data were baseline-corrected with respect to the 200 ms pre-stimulus interval and digitally low pass filtered at 20 Hz. Epochs containing artifacts were excluded from further analysis. Analysis was based only on trials with correct responses. Data were averaged over matches and nonmatches, because we were interested in the retention interval, a period in which these two types of trials are not yet discriminable for the subjects and so processing is the same.

We calculated contralateral and ipsilateral slow potentials as well as the CDA as described in Experiment 1 (Chapter 5.2.4).

6.3 Results

All data were analyzed by analysis of variance (ANOVA) and if applicable corrected for non-sphericity using the Greenhouse-Geisser-correction (Greenhouse & Geisser, 1959). If the correction was adopted, we report Greenhouse-Geisser epsilons (ε) and corrected *p*-values (p_{corr}) together with the original *F*-values and original degrees of freedom. Effects and interactions were further decomposed by nested ANOVAs and testing of polynomial trends and contrasts. In all graphs, 95%-confidence intervals are calculated according to the procedure described by Jarmasz and Hollands (2009) and are based on the error term of the respective effect of interest. We corrected the critical *t*-values' *df*s appropriately if εs were too low, as suggested by Loftus and Masson (1994). The effects on which the confidence intervals are based on can be found below each figure.

6.3.1 Behavioral data

Mean performance accuracy for all conditions is shown in Table 6.1. Performance declined with increasing number of relevant items. A 3 (*number of relevant items*) × 3 (*number of irrelevant items*)-ANOVA on mean accuracies confirmed a significant effect of number of relevant items, $F(2,28) = 23.22$, $\varepsilon = .63$, $p_{corr} < .001$, $\eta^2_{partial} = .62$, indicating a decrease in accuracy with higher memory load. There was no effect of number of irrelevant items nor an interaction of number of irrelevant by number of relevant items, $F(2,28) = 1.33$, $\varepsilon = .94$, $p_{corr} = .28$, $\eta^2_{partial} = .09$, and $F(4,56) = 1.84$, $\varepsilon = .75$, $p_{corr} = .16$, $\eta^2_{partial} = .12$, respectively. All levels of the factor number of relevant items differed significantly from each other (all *p*s < .05).

Table 6.1

Mean Accuracies as a Function of the Number of Relevant and the Number of Irrelevant Items.

Number of	Number of relevant items		
irrelevant items	1	2	3
1	.965	.941	.923
2	.961	.966	.924
3	.964	.952	.921

6.3.2 Electrophysiological data

Analyses were based on mean voltage amplitudes averaged over the time window from 350 to 700 ms after the onset of the memory array.

As anticipated, the number of relevant items had the strongest effect on activity measured over electrodes at posterior recording sites, especially at P3/4, P5/6, P7/8, PO3/4 and PO7/8.

We consequently pooled over these five electrode sites separately for contralateral and ipsilateral activity and for the CDA.

Effects of the number of relevant and irrelevant items were analyzed for contralateral slow potentials, ipsilateral slow potentials and the CDA separately by three 3 (number of relevant items) × 3 (number of irrelevant items)-ANOVAs.

The contralateral slow potentials are shown in Figure 6.2. A 3 (number of relevant items) × 3 (number of irrelevant items)-ANOVA on the mean amplitude of slow potentials over the hemisphere contralateral to the relevant hemifield revealed a main effect of number of relevant items, $F(2,28) = 26.45$, $\varepsilon = .65$, $p_{\text{corr}} < .001$, $\eta^2_{\text{partial}} = .65$, and a significant interaction of number of relevant items by number of irrelevant items, $F(4,56) = 5.12$, $\varepsilon = .84$, $p_{\text{corr}} < .01$, $\eta^2_{\text{partial}} = .27$. A clear linear increase in the slow potentials' negativity as a function of the number of relevant items is evident in Figure 6.3. As can be seen in Figure 6.3, this increase is absent for the number of irrelevant items. Linear trend analyses confirmed this picture: contralateral slow potentials showed a significant linear trend for number of relevant items, $F(1,14) = 31.16$, $p < .001$ but no linear trend for number of irrelevant items, $F(1,14) = 0.43$, $p = .52$. Deconstructing the interaction, when only one relevant item is presented there was an effect of the number of irrelevant items $F(2,28) = 5.68$, $\varepsilon = .85$, $p_{\text{corr}} < .05$, $\eta^2_{\text{partial}} = .29$, namely the slow potential amplitude for one irrelevant item was significantly more positive than for two or for three irrelevant items, $F(1,14) = 5.02$, $p < .05$ and $F(1,14) = 7.88$, $p < .05$, respectively. Amplitudes were not influenced by the number of irrelevant items for two and three relevant items, $F(2,28) = 2.45$, $\varepsilon = .86$, $p_{\text{corr}} = .11$, $\eta^2_{\text{partial}} = .15$ and $F(2,28) = 0.01$, $p = .99$, $\eta^2_{\text{partial}} < .01$, respectively.

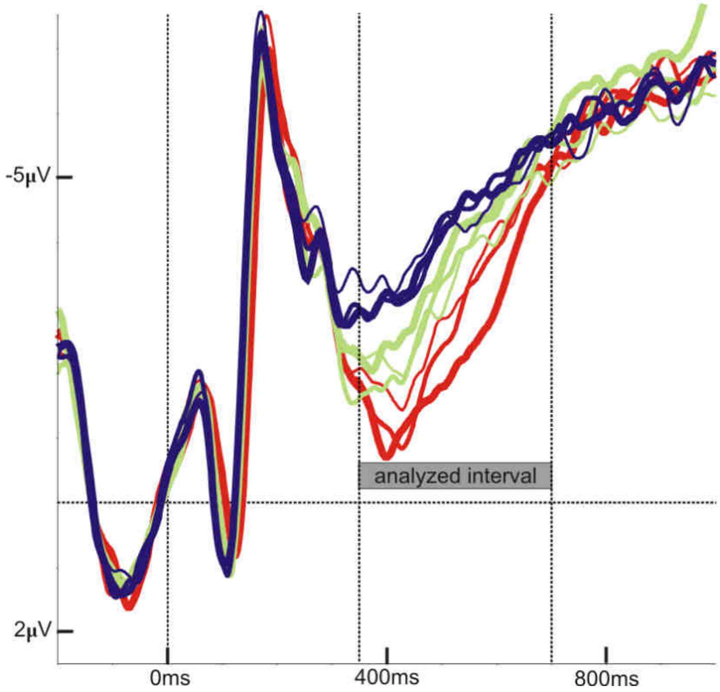

Figure 6.2. Grand averaged contralateral slow potentials relative to the onset of the memory array at posterior ROI (P3/4, P5/6, P7/8, PO3/4, PO7/8). Colors code the number of relevant items (red, one relevant item; green, two relevant items; blue, three relevant items) and line thickness codes the number of irrelevant items (thick, one irrelevant item; middle, two irrelevant items; thin, three irrelevant items).

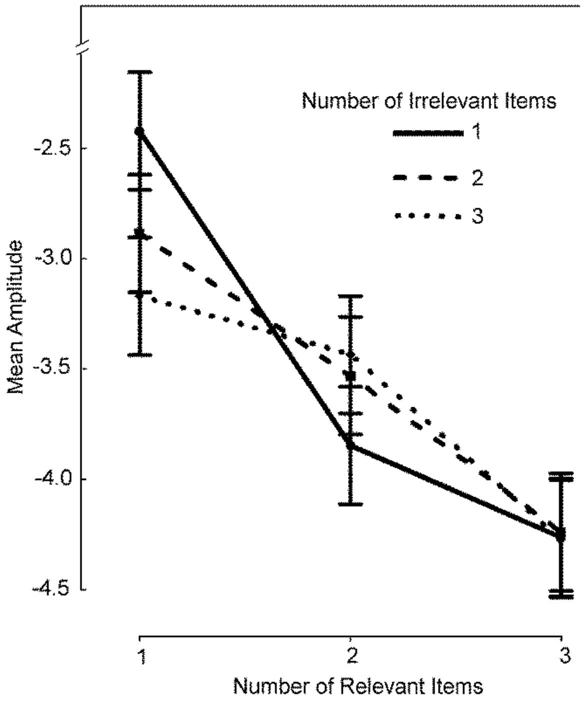

Figure 6.3. Contralateral slow potentials as a function of the number of relevant and irrelevant items averaged 350-700 ms after onset of memory array. The displayed 95%-confidence intervals are based on the interaction between number of relevant and irrelevant items.

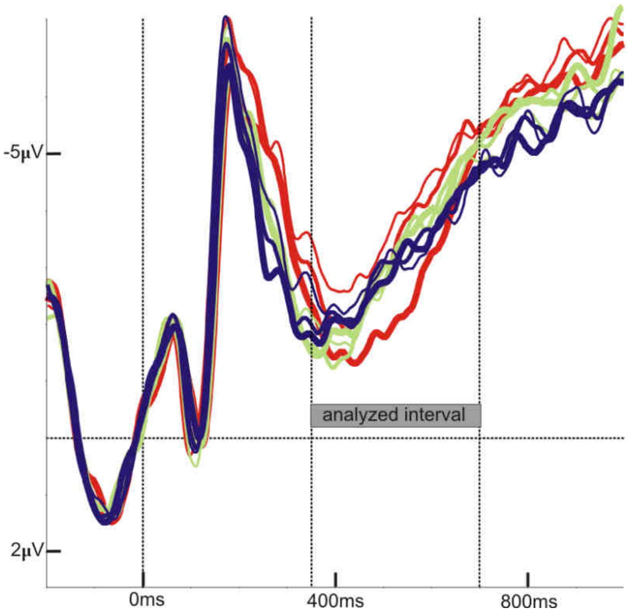

Figure 6.4. Grand averaged ipsilateral slow potentials relative to the onset of the memory array at posterior ROI (P3/4, P5/6, P7/8, PO3/4, PO7/8). Colors code the number of relevant items (red, one relevant item; green, two relevant items; blue, three relevant items) and line thickness codes the number of irrelevant items (thick, one irrelevant item; middle, two irrelevant items; thin, three irrelevant items).

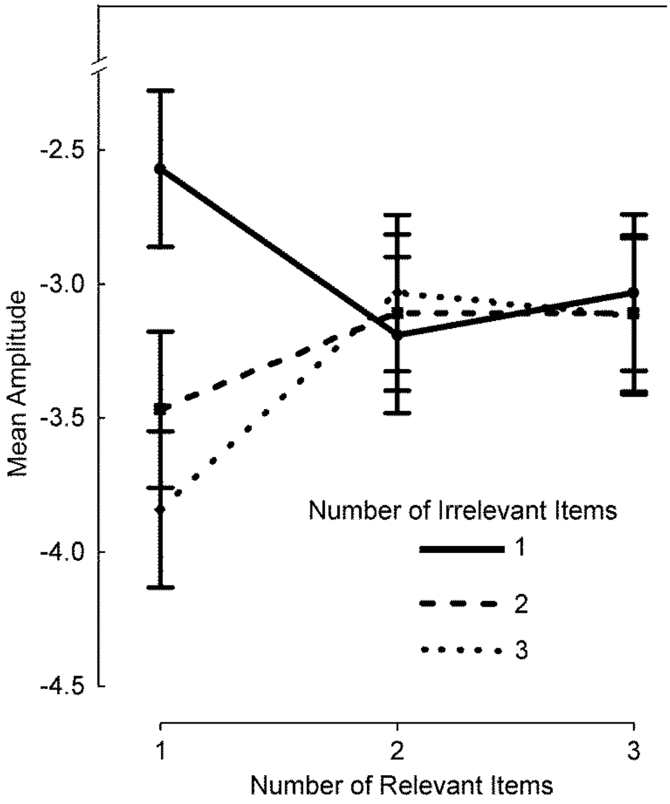

Figure 6.5. Ipsilateral slow potentials as a function of the number of relevant and irrelevant items averaged 350-700 ms after onset of memory array. The displayed 95%-confidence intervals are based on the interaction between number of relevant and irrelevant items.

A 3 (number of relevant items) × 3 (number of irrelevant items)-ANOVA on mean amplitudes of slow potentials over the hemisphere ipsilateral to the relevant items (see Figure 6.4 and 6.5) yielded a significant interaction for number of relevant items by number of irrelevant items only, $F(4,56) = 7.32$, $\varepsilon = .75$, $p_{\text{corr}} < .001$, $\eta^2_{\text{partial}} = .34$. Notably, there was no main effect for the number of relevant items, $F(2,28) = 0.71$, $\varepsilon = .86$, $p_{\text{corr}} = .48$, $\eta^2_{\text{partial}} = .05$. Deconstructing the interaction, when only one relevant item was presented, the number of irrelevant items modulated the amplitude of slow potentials over the ipsilateral hemisphere, $F(2,28) = 13.89$, $p < .001$, $\eta^2_{\text{partial}} = .50$. This effect was due to slow potential amplitudes for one irrelevant item being more negative than those for two or three irrelevant items, $F(1,14) = 12.51$, $p < .01$ and $F(1,14) = 26.56$, $p < .001$, respectively. This ipsilateral amplitude modulation was absent when two or three relevant items were presented, $F(2,28) = 0.18$, $\varepsilon = .89$, $p_{\text{corr}} = .81$, $\eta^2_{\text{partial}} = .01$ and $F(2,28) = 0.08$, $p = .92$, $\eta^2_{\text{partial}} = .006$, respectively.

The mean amplitude of the CDA as a function of the number of relevant and irrelevant items is shown in Figure 6.6. As can be seen from Figure 6.6, the CDA is clearly modulated by the number of relevant items; its amplitude becomes more negative with higher memory load. To estimate the effects of the number of relevant and irrelevant items we computed a 3 (number of relevant items) × 3 (number of irrelevant items)-ANOVA. The main effect of number of relevant items, $F(2,28) = 33.97$, $\varepsilon = .65$, $p_{\text{corr}} < .001$, $\eta^2_{\text{partial}} = .71$, reflects the increasing negativity of CDA amplitude with increasing number of relevant items. Linear trend analysis confirmed this picture, $F(1,14) = 40.03$, $p < .001$. Furthermore, a main effect of number of irrelevant items, $F(2,28) = 3.68$, $\varepsilon = .98$, $p_{\text{corr}} < .05$, $\eta^2_{\text{partial}} = .21$, was present. CDA amplitude was more negative for one irrelevant item as compared to two or three irrelevant items, $F(1,14) = 5.71$, $p < .05$ and $F(1,14) = 5.94$, $p < .05$, respectively[2].

As was expected based on the results of the analyses of the contralateral and ipsilateral slow potentials, a 2 (two vs. three relevant items) × 3 (number of irrelevant items)-ANOVA revealed an effect of the number of relevant items only, $F(1,14) = 27.29$, $p < .001$, $\eta^2_{\text{partial}} = .66$. CDA amplitude was more negative for three compared to two relevant items. In contrast, an effect of the number of irrelevant items and an interaction were absent, $F(2,28) = 1.33$, $p = .28$, $\eta^2_{\text{partial}} = .09$ and $F(2,28) = 0.38$, $p = .69$, $\eta^2_{\text{partial}} = .03$, respectively.

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[2] The CDA amplitude is more negative for one irrelevant item compared to two or three irrelevant items at three out of five electrodes only (P3/4, PO3/4, PO7/8). For the other two electrodes (P5/6, P7/8), there is no effect for the irrelevant items on CDA amplitude. In contrast, all five electrodes show clear effects for the number of relevant items.

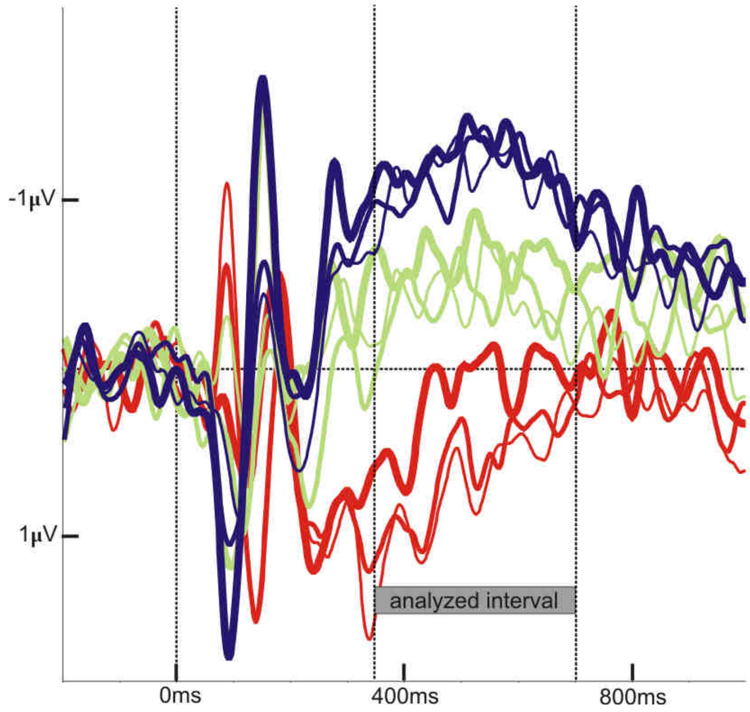

Figure 6.6. Grand averaged difference wave (CDA) relative to the onset of the memory array at posterior ROI (P3/4, P5/6, P7/8, PO3/4, PO7/8). Colors code the number of relevant items (red, one relevant item; green, two relevant items; blue, three relevant items) and line thickness codes the number of irrelevant items (thick, one irrelevant item; middle, two irrelevant items; thin, three irrelevant items).

6.4 Discussion

The amplitude of posterior slow potentials, measured during the retention interval of change detection tasks, is sensitive to the amount of processed items. We exploited this fact to find out, whether in addition to contralateral activity, also ipsilateral delay activity occurs in a lateralized change detection task, and if so, whether it reflects processing of the relevant or the irrelevant items. An influence of the amount of items on ipsilateral slow potentials was observed earlier (Robitaille et al., 2009). However, in lateralized change detection tasks the numbers of items in the relevant and irrelevant hemifields are usually the same. Therefore, the variation of the number of relevant or of the number of irrelevant items might have caused these amplitude modulations. By independently manipulating both numbers we were able to separately examine the influence of relevant and irrelevant items on slow potentials over the contra- and ipsilateral hemispheres.

In line with earlier studies (Klaver et al., 1999; Vogel & Machizawa, 2004; McCollough, 2007; Robitaille & Jolicoeur, 2006; Robitaille et al., 2009), during the retention interval, contralateral slow potentials as well as the CDA were modulated by the number of relevant items. Notably, in the present study the amplitude of the ipsilateral slow potentials was not modulated by the number of relevant items. This pattern of data suggests a completely lateralized memory effect for the relevant items.

In contrast to the strong electrophysiological effect of the number of relevant items, the number of irrelevant items had no effect on slow potentials. One exception is the condition in which only one item was to be remembered which will be discussed shortly. The absent effect of the number of irrelevant items suggests that, as instructed, participants ignored irrelevant items and focused on the relevant hemifield. Consequently, irrelevant items were filtered out and did not enter visual WM. Indeed, in the lateralized change detection task the specific filtering mechanism might be the allocation of attention towards the relevant hemifield. Accordingly, Hillyard et al. (1998) assume that selective attention biases the strength of a perceptual representation. Bundesen et al. (2005) theorize that more processing resources are available for objects that have gained a higher attentional weight. Consequently these objects are more likely to be encoded into visual WM. This is similar to Awh's hypothesis that attention works as a rehearsal mechanism in working memory (Awh & Jonides, 2001). When more than one item had to be processed in the present study, participants appear to have efficiently directed attention towards the relevant hemifield and biased processing in favor of the relevant items.

There was one important exception where the number of irrelevant items had an impact. When only one relevant item had to be processed, we observed amplitude modulations due to the number of irrelevant items over the hemisphere ipsilateral to the relevant hemifield, that is, over the hemisphere that received these items. This suggests that, in this condition, irrelevant items were not filtered out, but were processed to some extent. Critically, this effect cannot be explained by increased effort or task difficulty, because the amplitude of ipsilateral slow potentials should depend on the amount of relevant items, if this were the case. Obviously, when only one item is memorized, memory load is far from at its capacity limit. In this case, all information seems to be processed without filtering out of irrelevant information. The processing of irrelevant information might also cause the effect of the amount of irrelevant items on the slow potentials contralateral to the relevant hemifield when only one item has to be memorized because the available capacity is shared between relevant and irrelevant information.

From the results discussed in the two preceding paragraphs, it would appear that irrelevant items are processed when only one relevant item is present but are filtered out when visual WM load is higher. These results are in line with one theory forwarded by Lavie and colleagues (e.g., Lavie, 2005; Lavie, Hirst, De Fockert & Viding, 2004). They assume that when perceptual load is low, capacity that is not needed for the processing of relevant information automatically and involuntary spills over to the irrelevant stimuli. In contrast, when perceptual load is high, selective attention reduces distractor perception. In the lateralized change detection task, capacity might also involuntarily spill over to the irrelevant hemifield when one relevant item is shown. With more relevant items on the other hand selective attention might suppress this spread of capacity.

Our design, the orthogonal variation of the number of items in both hemifields, required the creation of a display which was unbalanced in perceptual terms. If perceptual effects on slow potential activity had been present, this aspect of our design would have allowed for an alternative interpretation of our results; then the effects of the number of items might have been driven by perceptual instead of mnemonic processes. However, from our data we can exclude this alternative. There were no effects of the number of irrelevant items when two or three relevant items were presented, although perceptual effects, if existent, should have been present in all conditions.

Several authors discuss changes in ipsilateral slow potential activity near the end of the retention interval (Robitaille et al., 2010; McCollough et al., 2007). A close look on Figure 6.4 reveals a modulation of the ipsilateral slow potentials as a function of the number of relevant items in the last section of the retention interval. However, in contrast to all memory-related effects in our study and in contrast to all earlier research on memory processes during the lateralized change detection task, the ipsilateral slow potentials' amplitude becomes more positive with increasing number of relevant items. Given this pattern, it is rather improbable that the amplitude modulation of ipsilateral slow potentials in this late time window is related to the process of maintaining items in visual WM. McCollough et al. (2007) discuss an increase in ipsilateral activity at the end of the retention interval as an anticipation process for the upcoming test array. Also the late ipsilateral activity observed in the present study might be related to an anticipation of the test array. As these late effects seem not to reflect memory processes, they do not affect our interpretation of the earlier memory-related effects. Further research is necessary in order to understand these late processes and their contribution to a successful handling of the change detection task.

The present study leads to three important conclusions: (1) Variation of the number of relevant items caused amplitude modulations over the hemisphere contralateral to the relevant hemifield only. This suggests a complete lateralized processing of relevant items. Amplitude modulations ipsilateral to the relevant hemifield are exclusively caused by irrelevant items. (2) The amplitude of slow potentials measured over the hemisphere ipsilateral to the relevant hemifield was influenced by the number of irrelevant items when visual WM load was low, indicating that irrelevant items are not filtered out in this case. This might come about somewhat passively when the bottom-up capturing of attention by the onset of irrelevant stimuli is not prevented. In contrast, the number of irrelevant items did not influence slow potential amplitude when the load was high, indicating that irrelevant items were completely filtered out. Voluntary allocation of attention might work as a filter mechanism when visual WM load is high. (3) For extracting the CDA, these ipsilateral slow potentials are subtracted from contralateral ones. Our findings for ipsilateral slow potentials therefore suggest, that, when memory load is high, the CDA amplitude is only influenced by the number of relevant items; when only one item has to be remembered, the CDA amplitude is also influenced by the number of irrelevant items. Consequently, the CDA amplitudes for low and high memory load might not be directly comparable, because they might reflect only partially overlapping processes. However, according to our data, this problem does not apply to memory loads above one item, because in these cases the CDA purely reflects processing of relevant items.

In the lateralized change detection task, only the items in the relevant hemifield have to be maintained whereas the items in the irrelevant hemifield have to be ignored. In the current experiment we observed that participants were able to filter out these irrelevant items when necessary. Another approach to investigate selection mechanisms is to present irrelevant items also within the relevant hemifield. The investigation of this latter type of filtering will be the focus of the next part of this work.

Part 3

Plasticity of Selection Mechanisms in Visual Working Memory

7 Selection Mechanisms in Visual Working Memory

Humans are permanently confronted with a massive flow of incoming information. Most of this information is irrelevant for their current goals. Fortunately, they can to a certain degree ignore irrelevant information and focus their attention on specific activities, as for example reading books in public swimming pools, driving cars on busy roads or talking to friends in noisy restaurants. The ability to extract relevant information is also crucial for storage of information in visual working memory. It is possible to exert some control over which information to select and which information to ignore, with selection mechanisms that regulate access to visual WM. Well working selection mechanisms enhance visual WM efficiency. When persons are able to filter irrelevant information out, their limited WM capacity is reserved for relevant information only. Contrary, if irrelevant information is stored in visual WM, that means if the selection mechanisms work inefficient, then the available capacity is spent for relevant as well as irrelevant information. As selection mechanisms constitute such a crucial factor in visual WM, we set out to investigate whether they can be improved.

7.1 The Investigation of Selection Mechanisms in Visual Working Memory via the Lateralized Change Detection Task

With the aid of the lateralized change detection task, it is also possible to measure participants' filter ability. For this purpose, in addition to the to-be-remembered items (*targets*), irrelevant items (*distractors*) are added to the memory and test array. Participants are told how to distinguish the targets from the distractors; for example, targets can be spatially cued or can differ in shape from the distractors (e.g., Vogel et al., 2005). Participants' task is to remember the targets only and to ignore the distractors. With the aid of accuracy data as well as the here investigated electrophysiological measures, the posterior slow potentials and the CDA, one can measure how many items are actually held in visual WM. Consequently, one can infer how efficiently the distractors are filtered out (Vogel et al., 2005; Fukuda & Vogel, 2009). Employing this *lateralized change detection task with distractors* and measuring CDA amplitude as the dependent variable, Vogel et al. (2005) showed that the efficiency of selection mechanisms varied substantially across individuals. To show this, they employed a design with (a) two targets and (b) four targets and (c) two targets together with two to be inhibited distractors; (a) and (b) constitute *pure-target trials*, (c) a *distractor-present trial*. The objects were red and blue bars with different orientations, red bars were defined as targets, blue bars as distractors and participants were instructed to maintain only the red bars in memory. During test, they decided whether one target has changed its orientation or all targets remained in their original orientation. The distractors never changed from memory to test array. If, on the one hand, in the distractor-present trials, participants were perfectly able to ignore the two distractors and only focus on the two targets, their CDA amplitude as a marker of items maintained in visual WM should equal the CDA amplitude for the condition with two targets only. If, on the other hand, participants' selection mechanisms were not effective and they additionally remembered the irrelevant distractors, their CDA amplitude in distractor-present conditions should equal the CDA amplitude for the condition with four targets.

The pattern of CDA amplitude varied across participants. The authors divided their subject sample into two halves based on their personal visual WM capacity as estimated with the aid of the behavioral K-index. Subjects with high visual WM capacity showed a CDA amplitude that was equivalent for array sizes of two items and array sizes of two items and two distractors, suggesting that they efficiently selected targets from among distractors and consequently remembered the targets only. In contrast, subjects with low visual WM capacity showed a CDA amplitude for array sizes of two targets and two distractors that was as high as the CDA amplitude for array sizes of four targets. These participants seemed unable to protect their WM against irrelevant distractors. This relation is also expressed in a significant correlation between the behavioral K-index and an index of filter ability extracted from the CDA amplitude pattern (for details concerning the calculation of this filter index, see Vogel et al., 2005).

Further testing excluded the possibility that the results were observed only due to the specific design of selecting distractors on the basis of their color. The authors used the same lateralized change detection design, but filtering affordances were realized via location (Vogel et al., 2005) or via shapes (Fukuda & Vogel, 2009). When participants had to filter irrelevant items by location, at the beginning of a distractor-present trial an arrow pointed not straight to the right or left as in pure-target trials, but either in the upper or the lower quadrant of the relevant hemifield. Items were presented in both quadrants and the items in the quadrant where the arrow pointed to were defined as the targets, the remaining ones were the distractors. In a further version of the lateralized change detection task with pure-target trials and distractor-present trials, Fukuda and Vogel (2009) used colored squares and rectangles. Participants' task was to remember the colors of the squares only (targets) and ignore the rectangles (distractors). In both studies, CDA amplitudes were a valid measure of items maintained in visual WM and hence allowed inferences about participants' filter efficiency.

7.2 Selective Attention as the Process Underlying Successful Selection in Visual Working Memory

A crucial question is how the process of filtering in the lateralized change detection task with distractors actually works. As already discussed above (see Chapter 7.1), Vogel and colleagues (Vogel et al., 2005; Fukuda & Vogel, 2009) showed that participants differ in their ability to protect their limited available visual WM capacity against distracting information and that this is reflected in CDA amplitudes. Fukuda and Vogel (2009) investigated the question whether involuntary attentional capture through distractors has consequences for later processing in visual WM and thus accounts for the differences in filter ability between participants. They employed the version of the task already discussed in the last chapter (Chapter 8.1), where participants had to remember the color of squares (targets) and ignore the rectangles (distractors). They ran pure-target trials with two or six targets and distractor-present trials with two targets and four distractors.

The *dot probe technique* allows measuring the allocation of attention in the display at a specific time point. The logic is that shortly appearing dots are more probably detected when attention already dwells at the location where they appear than when attention is directed to another location in the display. When measuring the EEG, components can be extracted that indicate attentional allocation in the display at the point of the appearance of the dot. At locations in the display where attention is currently focused, amplitude as a response to the dot should be strongly increased. The authors deployed this technique during the change detection task with distractors to learn about participants' attention allocation towards targets and distractors shortly after their presentation on the screen. 50 ms after onset of the retention interval a little white square (the probe) appeared in each hemifield, either on target or on distractor locations. As an indicator of attention the authors measured the N1/P1 component from 75-175 ms after presentation of the probe array. The authors reasoned, that if participants are able to prevent attentional capture through the irrelevant distractors, their attention should be focused towards the targets. In that case, probes on target locations should lead to a more pronounced N1/P1 amplitude as compared to probes on distractor locations. If in contrast, participants are captured through the distractors the N1/P1 amplitudes in response to dots on target and distractor locations should be similar. The authors defined the attentional capture effect as the mean difference in N1/P1 amplitude between probes at target locations and probes at distractor locations. If this value is high, the respective participant is well able to focus his attention towards targets only. They used the CDA as an indicator of storage in visual WM and calculated a filter index from the CDA pattern (for details concerning the exact calculation of this filter index, which deviated from the calculation employed in Vogel et al., 2005, see Fukuda & Vogel, 2009). Interestingly, they observed a significant correlation between the attentional capture effect and this index of filtering in visual WM. Participants who were better able to protect their scares memory resources against attentional capture through distractors later showed less unnecessary storage of these distractors. Furthermore, both effects, the attentional capture and the unnecessary storage correlated with behaviorally measured visual WM capacity. Although no statements about causality are possible, this is suggestive evidence that the early selection mechanism strongly influences visual WM functioning in the presence of distractors. How well participants are able to prevent attentional capture through distractors in this early time interval is a strong predictor of filter abilities in visual WM.

To sum up, competent selection mechanisms are vital for the efficient processing of relevant information in the presence of distractors in visual WM. The lateralized change detection task and the associated electrophysiological component, the CDA, turned out as a useful tool in examining selection mechanisms in visual WM (Vogel et al., 2005). Crucial for the prevention of distractor storage in visual WM seems to be the allocation of attention towards the targets and the prevention of attentional capture through distractors (Fukuda & Vogel, 2009). The ability to selectively focus attention towards targets might be sensitive to training. Although, until now, there are no studies in which selection mechanisms in visual WM have been trained successfully, we will have a closer look on the method of WM-training in general and how it can be utilized for our aim to improve selection mechanisms in visual WM.

8 Training Studies as a Tool to Investigate Working Memory

Over the last decades cognitive training has developed as a favored tool in experimental psychology for two reasons. Firstly, there is a plenty of research on plasticity of cognitive functions, such as attention, working memory, dual tasking, fluid intelligence etc. to enhance the functioning of these abilities and thereby the quality of daily life. Often specific samples, such as children with ADHD, stroke patients, mentally disabled, and psychiatric patients, are in the spotlight of such interventions. Secondly, from a cognitive perspective, training studies are used to investigate the plasticity of cognitive constructs or to disentangle specific systems or processes. Within the scope of the current dissertation project we will focus on the training of WM. We are particularly interested in the latter approach to disentangle a specific process, because we aim to specifically train filtering in visual WM. A growing body of WM-training studies has crystallized out that WM functioning is improvable indeed, leading to performance enhancements and changes in neural activity of associated brain structures.

8.1 Training Batteries

One popular approach to WM training are large training batteries. These studies target the training of several WM tasks often within different modalities and sometimes among other cognitive tasks (e.g., Chein & Morrison, 2010; Klingberg, et al., 2005; Westerberg & Klingberg, 2007; Schmiedek, Lövden & Lindenberger, 2010). These studies consistently find that WM is indeed trainable; they report performance improvements in the trained WM-tasks. Additional to these observed improvements in trained tasks, one further important feature of a successful intervention is its transfer to other tasks measuring higher cognition, as evident in most of these training batteries (see Morrison & Chein, 2011 for a review). One much-noticed finding is the successful transfer to measures of fluid intelligence (e.g., Klingberg et al., 2005; Olesen, Westerberg & Klingberg, 2004; Westerberg & Klingberg, 2007; Schmiedek, Lövdén & Lindenberger, 2010; but see Chein & Morrison, 2010). Additionally, there is also transfer to measures of response inhibition (Klingberg et al., 2005; Westerberg & Klingberg, 2007; Chein & Morrison, 2010) and measures of reading comprehension (Chein & Morrison, 2010). The underlying hypothesis is that if higher cognitive processes are trained and not only task-specific or modality-specific ones, a transfer to other higher cognition-demanding tasks is most likely. This touches an important advantage of the training-batteries in their aim of an effective intervention. The variety of the trained tasks makes training gains and successful transfer probable. Firstly, the variety of tasks with different cognitive requirements and within different modalities precludes simple strategy-effects or effects of automatization. Secondly, it appears that modality- and domain-unspecific processes are trained whose functioning influences many cognitive domains. This leads to one of the utmost disadvantages of these training-batteries, at least from a cognitive view: The bandwidth of trained tasks renders it completely impossible to make statements about what exactly was trained.

8.2 Training of Specific Working Memory Tasks

Another approach is not to train large batteries of WM tasks, but one specific WM-task or a small number of related WM-task, accompanied by specific hypotheses concerning training-specific changes. This approach allows for making statements about what underlying cognitive functions are enhanced through training. One advantage of these studies above the battery-training is the possibility to prove that the training really changed processes associated with WM proper and not other task-related processes. This approach is often supported by neuroimaging methods. For example, Olesen et al. (2004) measured fMRI before, during and after WM-training. They observed training-induced activity increases in frontal and parietal cortices. That these activity increases are in regions beforehand identified as associated with WM processes is a nice confirmation for the assumption that they are specifically related to WM functioning. However, the authors concede that no inferences can be drawn concerning the specific functioning of the identified regions. Furthermore, Moore, Cohen and Ranganath (2006) trained their participants to become experts in a specific category of new complex objects. Thereafter, participants performed a WM-task with this category and a further, non-trained category while they were scanned. Participants performed better in the trained category and this effect of expertise was reflected in the neuronal correlates in occipitotemporal cortices and prefrontal and posterior parietal networks. The authors infer that WM functioning was improved via expertise reflected in a better object recognition controlled in structures of occipitotemporal cortices and the development of a frontoparietal network possibly controlling domain-specific WM processes.

Regarding the observation of successful transfer, positive results are much scarcer in these latter training studies as compared to the training batteries, which is actually expectable. As WM-training focuses on only one or a few tasks, the range of trained processes is more constrained. One study reporting successful transfer to measures of fluid intelligence used a dual *n*-back task with a visuospatial and a phonological part as training task (Jaeggi, Buschkuehl, Jonides & Perrig, 2008). In the course of training participants got continuously better in the dual *n*-back task and additionally to this training gain they improved their performance in a measure of fluid intelligence. The authors discuss that transfer might have occurred as many executive processes and less strategies or automatization was trained. These executive processes, first of all controlled attention, might also be necessary to solve tests of fluid intelligence. However, we remain with the same résumé as for the preceding studies: Exactly which process improved during training and played a crucial role in both training and transfer task remains unclear. This is where the real beauty of training tasks, from the view of the cognitive sciences, comes to light. With the aid of a suitable design, it is possible to disentangle specific WM-processes.

8.3 Process-Specific Training

These studies aim to single out and improve the functioning of a particular process of interest via the specific training of this process. Dahlin, Neely, Larsson, Bäckman & Nyberg (2008) aimed to train the specific executive process of updating via a letter-memory-updating task and to find transfer to an *n*-back task, known to require the process of updating, too. As a control task the authors employed the Stroop task, a task that also requires executive processes, but not the specific process of updating. The authors made use of the knowledge that the brain region associated with updating is the striatum. Accordingly, in the pre training session, they observed striatum-activity in the letter-memory-updating and the *n*-back task, but not in the Stroop task. Through training the performance and striatum activity in the letter-memory task increased. The authors observed a transfer to the *n*-back task in form of higher performance and increased striatum activity after training, but not to the Stroop task. They therefore concluded that training-induced improvements in the particular process of updating are responsible for the observed transfer effects. Persson and Reuter-Lorenz (2008) aimed to specifically train the process of interference resolution in WM. To disentangle this specific process the authors employed three groups. One trained WM tasks with high interference, one trained WM tasks with low interference and a third group trained tasks with low demands on both, WM and interference resolution. They argued that if on the one hand WM-training alone improves interference resolution, the first two groups should show training gains in interference resolution and transfer to other tasks also demanding this process of interest. If on the other hand, only the specific training of interference resolution works, only the group training WM tasks with high demands on this process should show training and transfer effects. Unfortunately, the authors had to retract their article, because observed training and transfer effects have crystallized out not to be caused by improved interference resolution. The authors explain the observed effects with a programming error and were not able to replicate the effects after the mistake in the program was eliminated.

A further important question often addressed by WM-training is the disentangling of modality-specific and cross-modal processes. Schneiders, Opitz, Krick and Mecklinger (2011) separated modality-specific (visual and verbal) working memory processes from domain-general processes. One group of participants trained a visual *n*-back task, the other group trained an auditory *n*-back task; the third group was a no-contact control group. After training, both training groups were better than the control group in a visual *n*-back task, but the visual-training group had larger performance increases in this task as compared to the auditory-training group. The authors report training related decreases in frontal activity for the visual-training group only, which they interpreted as modality-specific effects. Furthermore, training related decreases in frontal and parietal activity were observed for both groups, and hence interpreted as improvements in executive functions. A behavioral study of Walther (2012), used a similar design, but tested all three groups with a visual and an auditory version of the *n*-back task. Both, the visual-training and the auditory-training group outperformed the control group in the post-training session, but their performance accuracy was absolutely equal in both versions of the *n*-back task. Independent of the training-modality, both groups showed perfect transfer to the other modality, indicating that cross-modal processes have been trained.

Unfortunately, up to now, only few process-specific training studies were conducted. Much more research is desirable because these training studies are a powerful tool for the disentanglement of processes associated with WM functioning and their specific training.

8.4 Important Aspects of a Training Study Design

From the existing literature, it is nearly impossible to infer the prevailing principles for the design of a “good” training study. Unfortunately, for a systematic validation there are not yet enough training studies and the existing ones are too heterogeneous with respect to duration of training, type of training (adaptive or non-adaptive), type of tasks, type of transfer (near- or far-transfer), used subject sample, etc. Much more systematic research is required to be able to make clear statements about adequate training designs. However, there seems to be some consensus regarding several important components of a training study that are important for design decisions concerning our training study. These components are the merits of adaptive training, the usability of no-contact versus active control groups, the importance of long-lasting effects and their validation and the anticipation of transfer.

Adaptive training

Concerning the first point, adaptive training designs are discussed as being superior to non-adaptive ones (see Morrison & Chein, 2011; Klingberg, 2010). In line with this reasoning nearly all training studies discussed above employ an adaptive design (e.g., Holmes et al., 2009; Jaeggi et al., 2008; Klingberg et al., 2005; Schneiders et al., 2011), reflecting its acceptance in the community as the better choice. It seems plausible that a task whose difficulty level is continuously adapted to the respective performance level of each participant leads to the maximum training-effectiveness. One the one hand, the task remains demanding for each participant and the development of specific strategies or automatization can be avoided. On the other hand, the task does not require overcharging demands for less well performing participants and mental overload can be avoided. Adaptive designs should also preserve participants’ commitment, an important building block of a successful training study. Morrison and Chein (2011) discuss that absent training gains in the study of Olson and Jiang (2004) might be due to their non-adaptive training. However, not much systematic research was yet conducted on the differential effectiveness of adaptive and non-adaptive designs. Directly comparing adaptive to non-adaptive WM training in children revealed a significant difference in training gains; adaptive training was more effective (Holmes, Gathercole & Dunning, 2009). It remains to be mentioned that the non-adaptive version was a really easy one as compared to the adaptive one. A comparison between two challenging tasks, one adaptive and the other not would further enlighten this question.

Type of control group

Employing a control group is indispensable in a training study, because otherwise true training-related interventions could not be disentangled from mere retest-effects. There are two types of control group: no-contact control groups and active control groups. An active control group is the best choice when WM-training is “unspecific” in terms of the process of interest. The mere knowledge to belong to the training group might evoke placebo-effects (cf. Klingberg, 2010). Differences between the training and the no-contact control group might therefore not clearly be attributable to training effects. To prevent this problem, often an active control group that trains a non-adaptive, not challenging and shorter version of the training group’s training task is employed (see Klingberg, 2010 for a review). Although this is theoretically reasonable, one must consider the practical problem that the control group eventually has to do some very boring task for several days, as for example a 0-back task, and that this underemployment might also have negative effects. A no-contact control group is suitable in a design with very specific hypotheses concerning the course of training or the trained process. When the researcher has clear hypotheses instead of expecting unspecific training gains, a no-contact control group is sufficient to disentangle possible placebo-effects from true training gains. For example, in the study of Dahlin et al. (2008) it is not reasonable to assume that the specific improvements in updating ability are a consequence of mere placebo-effects.

Validation of long-term training gains

One important validation of a successful training is the durability of observed training-gains and transfer over time. That is why most training-studies evaluate their training gains and observed transfer in a follow-up study several months after training (e.g., Holmes et al., 2009; Klingberg et al., 2005). Westerberg & Klingberg (2007) discuss that a steady performance improvement over training sessions and long-lasting training-effects is best brought into accordance with skill acquisition and not the mere training of strategies.

Performance improvements and activity changes of brain areas associated with constructs such as WM, attention, reasoning, interference resolution, etc. should still be measurable a considerable time after training to support strong claims of cortical plasticity. From an application-oriented point of view, long-lasting effects of training and transfer are obviously preferable because any intervention is desired to affect and improve functioning in daily life (for a similar discussion regarding the transfer effects to fluid intelligence see Sternberg, 2008).

Transfer effects

What kind of training successfully leads to transfer is a question most researchers of training studies are concerned with. The transfer within a specific domain and a specific modality, such as visual WM, to other stimuli or a slightly different task is considered as near-transfer. Far-transfer refers to transfer to other modalities, for example from visual WM to phonological WM, or to transfer to other cognitive constructs, for example from WM-training to fluid intelligence.

But what exactly are the conditions under which transfer is to be expected? A training of domain-general processes (e.g. via large training batteries) seems to increase the probability of transfer as compared to training of modality-specific processes. Klingberg (2010) reasons that far-transfer reflects improvements in a common neural WM-network. When only very circumscribed processes of interest are trained, special care must be taken that trained and transfer task both rely on these processes. For example, Oleson et al. (2004) observed a transfer from WM-training to the Stroop task. This behavioral transfer was reflected in increased brain activity in middle frontal gyrus, a brain area usually active in both tasks. A specific process needed for both tasks and reflected in activity in middle frontal gyrus might underlie the observed transfer (Jonides, 2004). The above reviewed training study of Dahlin et al. (2008; see Chapter 8.1.3) impressive example for the observation of transfer after the training of the specific process of updating and respective neuronal plasticity.

So far, as preparation for Experiment 3, two topics have been introduced in Part 3. Firstly, we discussed the relevance of selection mechanisms for efficient visual WM functioning and how this can be measured via the lateralized change detection task. Secondly, we presented a short overview on the method of training as a tool for the specific improvement of a visual WM process.

9 Experiment 3: Training of Selection Mechanisms in Visual Working Memory[3]

9.1 Introduction

The ability to filter out irrelevant information is crucial for successful visual WM performance. As detailed above (Chapter 7), visual WM capacity is highly limited and it is therefore advantageous to be able to exclude irrelevant information from being remembered, and thereby to preserve the available capacity for relevant information only. Competent selection mechanisms are thus vital for efficient visual WM. In view of the importance of these mechanisms, a critical issue is whether efficiency of visual WM can be improved by enhancing the ability to filter irrelevant information out of visual WM. To investigate the plasticity of selection mechanisms in visual WM, we conducted a training study. We used the lateralized change detection task with distractors to measure the efficiency of visual WM selection mechanisms before and after training. The design of the change detection task was similar to the one of Fukuda and Vogel (2009), as described above (see Chapter 7.1). We recorded behavioral as well as electrophysiological data to analyze changes in filter efficiency from pre- to post-training session. Based on the observation of Experiment 1 that incentive effects emerged in the posterior slow potentials and not in the CDA, we will examine both online measures of visual WM maintenance here.

We did not directly train a change detection task with filter demands, because this would make it hard to disentangle improvements in filter ability from a training of mere visual WM

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[3] Part of this chapter adapted from Arend and Zimmer (2012).

capacity. Subjects might automatically train both. A more appropriate training task for our requirements therefore, is a task which places high demands on filter ability but low demands on WM processes. In order to find an appropriate training task, a closer look on the selection mechanism at play in the change detection task with distractors is indicated. As already introduced above (Chapter 7.2), the specific process needed to perform this task is the ability to hold attention focused on the targets and prevent attentional capture through distractors (Fukuda & Vogel, 2009). Participants with low filter abilities are more likely to shift their attention away from the targets than those with high filter abilities (Fukuda & Vogel, 2009). As we search for a training task, demanding the same selection mechanisms as the change detection task, the appropriate training task for our demands needs the process of attention allocation. The multiple object tracking (MOT) task might fulfill these requirements.

The ability to hold sustained attention on targets and to prevent attentional capture through distractors is also highly important in MOT. The MOT task is an intensively studied visual attention task (e.g., Allen, McGeorge, Pearson & Milne, 2006; Cavanagh & Alvarez, 2005; Oksama & Hyönä, 2004; Pylyshyn & Storm, 1988; Pylyshyn, 2004; Scholl, 2009). At the beginning of each trial, several physically identical objects, usually circles, are presented. For a short time, some objects, the *targets* are highlighted to distinguish them from the rest of the objects, the *distractors*. Thereafter, targets and distractors, now indistinguishable again, move for several seconds within a defined array. Participants’ task is to track the targets and ignore the distractors. When the objects stop moving, participants have to select the targets. The dependent measure of interest is how many of the targets participants have successfully tracked and can therefore correctly select at the end of each trial. Many studies suggest that tracking performance depends on successful attention allocation. Several studies have found that distractors are attentionally inhibited during tracking (Pylyshyn, 2006; Pylyshyn, Haladjian, King & Reilly, 2008; Bettencourt & Somers, 2009). With the aid of electrophysiological methods, Drew and colleagues (Drew, McCollough, Horowitz & Vogel, 2009) found a significant attentional enhancement of the targets together with no suppression of distractors. They reasoned that poor trackers may have mistakenly tended to focus their attention on the distractors. Employing the same method, Doran and Hoffman (2010) found both an enhancement of targets and a suppression of distractors (see also Bettencourt & Somers, 2009).

Indeed, comparisons of the change detection task and the MOT task have revealed a close relationship between the two. First, the change detection and the MOT task have a similar mean capacity limit (cf. Cavanagh & Alvarez, 2005; Fougnie & Marois, 2006; Oksama & Hyönä, 2004; Pylyshyn & Storm, 1988; Vogel & Machizawa, 2004; Vogel, Woodman & Luck, 2001). Second, a MOT task performed during the retention interval of a change detection task created dual-task costs (Fougnie & Marois, 2006). Third, the CDA recorded during a lateralized MOT task, has been shown to persist during tracking and increased as a function of the number of tracked targets, being more negative for a higher number of tracked targets (Drew & Vogel, 2008). And last, in a direct comparison of the lateralized change detection task and the lateralized MOT task Drew, Horowitz, Wolfe, and Vogel (2011) found evidence for partially overlapping processes in both tasks. Both tasks revealed a CDA that was modulated by the number of remembered, respectively tracked, items. Furthermore, the authors report a CDA in both tasks with a similar spatial distribution and a similar relationship to performance. As highlighted above, the reason for our interest in MOT was that we searched for a training task requiring the same selection mechanisms as the change detection task with distractors. Drew et al. (2009) concluded that one important process that underlies performance in both tasks might be this common filter mechanism. As an overlap of processes of trained task and transfer task seems to be crucial for successful transfer (Dahlin et al., 2008; Jaeggi et al. 2008; Jonides, 2004; Klingberg, 2010), a successful training of filter ability in MOT should transfer to improved filter ability in the change detection task with distractors.

To our knowledge, there are currently no studies employing MOT as training task. However, there are indications that performance in MOT can be improved. For example, radar operators are better than students in MOT (Allen, McGeorge, Pearson & Milne, 2004). Furthermore, members of a university officer training corps are better in MOT then their fellow students (Barker, Allen & McGeorge, 2010). The authors reason that both groups of experts gain an advantage from their expertise in tracking objects due to affordances of their job or training. Pylyshyn (2006) reported evidence that four subjects that had considerable experience with the MOT task outperformed less experienced participants in allocating their attention towards the target locations. Furthermore, action video game training has been shown to transfer to MOT performance (Green & Bavelier, 2006). We therefore expected that training MOT will be effective and will lead to improved performance in this task. As adaptive training designs which increase demands as participants learn are discussed as potentially superior to non-adaptive ones (Klingberg, 2010), we increased filter demands with the progress of the participants. In order to ensure the MOT task trained predominantly filtering ability, we decided to manipulate the number of distractors. The number of distractors has shown to be one important variable in tracking performance. Performance in MOT decreases with an increasing number of distractors (Bettencourt & Somers, 2009; Horowitz et al., 2007; Oksama & Hyönä, 2004). Bettencourt and Somers (2009) have shown that this is not only due to crowding effects, that is, a denser display in which distractors more often approach attended targets, but instead, is in large part because of the higher demands on active selection mechanisms.

Subjects in the training group should improve their filter performance via adaptive MOT training. This should be evident in (a) a continuous advance to higher levels and (b) an initial drop in performance when a new level is reached. Over time, as participants' filtering abilities improve, they should learn to handle this increased number of distractors. If the specific filter process is the same for both tasks, successful training of this process in MOT, should lead to a transfer to filter efficiency in the change detection task with distractors. In the post-training session, for the training group, the efficiency of excluding distractors should have improved compared to the pre-training session. The number of maintained items in distractor-present conditions should approach the number of targets. The influence of distractors on accuracies as well as amplitudes of contralateral slow potentials and CDA should decline. The data pattern for distractor-present conditions should approach the data pattern of the respective low-load conditions and diverge from the respective high-load conditions. However, such an increase in performance might in principle also be due to the repeated performance of the change detection task. In order to control for such retest-effects we ran a second group of subjects who also took part in the pre- and post-training sessions but did not receive training in between (a no-contact control group).

9.2 Methods

In order to establish two participant groups with comparable scores in several cognitive measures, we conducted a first testing session several weeks before the start of the training study. During this session we collected several cognitive measures, including the K_{max} measured in a change detection task for colors which is a measure of a person’s WM capacity (Cowan, 2001), as well as an index of individual attentional abilities, measured in a paper and pencil test, the Frankfurter Aufmerksamkeits-Inventar (Frankfurt Attention Inventory, FAIR) (Moosbrugger & Oehlschlägel, 1996). According to these two indices, we assigned participants to the training and control groups as described below. During the pre- and the post-training sessions, which were separated by two weeks, participants in both groups performed a visual WM task, the lateralized change detection task with distractors, while their EEG was recorded. The training group performed a behavioral MOT training in between the pre- and the post-training session.

9.2.1 Participants

Fifty-nine students at Saarland University (7 left-handed, mean age: 24.51 years, range: 17-36, 38 female) participated in the first testing session. From this pool of 59 datasets, we created two groups of 20 participants each with equal means, $t(38) = 0.12$, $p = .91$, and, $t(38) = -.17$, $p = .87$, and variances, $F(1,38) = 1.03$, $p = .95$, and $F(1,38) = 1.07$, $p = .88$, in maximal K-indices and FAIR, respectively. One of these groups was randomly chosen as the training and the other as the control group. Consequently, in total 40 participants participated in the training study (7 left-handed, mean age: 25.13 years, range: 19-33, 27 female).

All participants had normal or corrected-to-normal vision. Participants were paid for their participation. For the first testing session, the pre- and the post-training session, participants received 10 € per hour for participation. The amount of additional payment participants in the training group received for the training sessions depended on their individual performance as detailed below. All participants gave informed consent after the nature of the study had been explained to them.

9.2.2 Pre- and post-training session

Stimuli

Stimuli were seven colored (red, blue, green, yellow, black, white, and purple) squares (targets) with a size of 0.65° x 0.65° and respective rectangles (distractors) with a size of 0.33° × 1.30° and were presented against a gray background. The stimuli appeared in two rectangular regions (4° × 7.3° each) that were centered 3° to the right and the left of the center of the screen.

Design and procedure

Participants performed a lateralized change detection task (see Figure 9.1). Before the presentation of the memory array, an arrow was presented for 200 ms. This arrow indicated which of the two hemifields was relevant and consequently had to be remembered. In 50% of the trials, the arrow pointed to the left, in the remaining 50% of the trials it pointed to the right. The memory array was presented for 100 ms and consisted of two rectangular regions, one in each hemifield. In each of these regions, two to five colored objects were presented. Within the rectangular regions, item positions were set at random with the limitation that the minimal distance between the centers of each pair of items was at least 2°. Within one trial, colors were randomly chosen with the constraint that a specific color could appear only once within one hemifield. Participants were seated at a distance of 70 cm from the monitor. Participants were instructed that the best method to encode the stimuli was to fixate on the central fixation cross and covertly move their attention to the side indicated by the arrow. We ran pure-target and distractor-present conditions. In the pure-target conditions, within the two hemifields two to five targets (2T, 3T, 4T, and 5T) were presented and all stimuli in the relevant hemifield had to be remembered. In the distractor-present conditions, within the two hemifields, targets as well as distractors were presented and only the targets in the relevant hemifield had to be remembered. We ran three distractor-present conditions, conditions with two targets and two distractors (2T2D), two targets and three distractors (2T3D) and three targets and two distractors (3T2D), within the two hemifields respectively. In 50% of the trials one of the squares in the relevant hemifield changed its color from memory to test array (*mismatch*), in the other half of trials all colors remained the same (*match*). Participants had to press one key to indicate a color change and another key when no color had changed, with their left and right hand, respectively. The assignment of keys to response class was counterbalanced across participants. All independent variables were varied within participants and randomized over all trials. This resulted in 100 trials per condition and 700 trials in total.

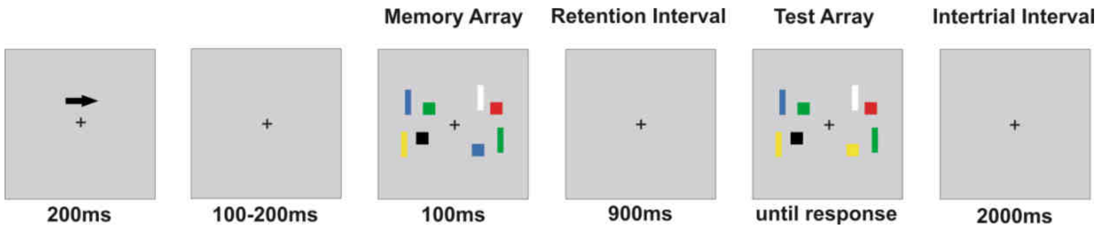

Figure 9.1. Schematic illustration of the task procedure. Depicted is a distractor-present trial.

In addition to the lateralized change detection task with distractors, participants performed a lateralized change detection task without distractors and on a separate day a test of fluid intelligence (Advanced Progressive Matrices; Kratzmeier & Horn, 1980) during the pre- and post-training session. The order of the two change detection tasks was counterbalanced across participants. As the change detection task without distractors is not directly relevant to the concerns of the present article, we do not report it further here.

EEG recording and analysis

The pre- and post-training sessions were run in a sound- and electromagnetically shielded chamber. EEG activity was recorded continuously from 38 Ag/AgCl electrodes (Easy Cap, Falk Minow Services, Germany) arranged according to the extended international 10-20 system. We recorded EEG at the following electrode sites: FPz, FP2, Fz, F4, F8, Cz, C4, CPz, CP4, T8, Pz, P2, P4, P6, P8, POz, PO4, PO8, Oz, O2 (and the respective left sites). Vertical and horizontal ocular artifacts were monitored by four ocular electrodes (above and below the right eye and at the outer canthi of both eyes). Impedances were kept below at least 10kΩ for EOG-electrodes and 5kΩ for all remaining electrodes. Signals were amplified with an AC coupled amplifier (Brain Amps, Brain Products, Munich), sampling rate was 1000 Hz with a 250 Hz analog low-pass filter and a time constant of 10 s. A left mastoid reference was used during recording and signals were re-referenced offline to the average of the signal at the mastoids. Occular artifacts were corrected according to Gratton, Coles and Donchin (1983). If the number of blinks was low, no correction was applied but the blink-contaminated trials were excluded.

ERPs were extracted by stimulus-locked signal averaging from -200 to 1000 ms relative to the onset of the memory array for each condition (2T, 3T, 4T, 5T, 2T2D, 2T3D, 3T2D). Data were baseline-corrected with respect to the 200 ms pre-stimulus interval and digitally low pass filtered at 20Hz. Epochs containing artifacts were excluded from further analysis. Analysis was based only on trials with correct responses. Data were averaged over matches and mismatches, because we were interested in the retention interval, a period in which subjects cannot yet discriminate between matches and mismatches.

We calculated contralateral and ipsilateral slow potentials as well as the CDA as detailed in Experiment 1 (see Chapter 5.2.4).

9.2.3 Training

Stimuli and motion algorithm

The stimuli in the training task were black circles with a diameter of 0.61°, moving within a gray bounding box of 11.47° × 11.47° in size. Circles moved with a speed in between -3 and 3 pixels in the horizontal and -3 and 3 pixels in the vertical direction per 2 refresh cycles (one motion step) of a 75 Hz monitor with a resolution of 1024 × 786 pixel and a size of 32 × 24 cm. The initial speed of each circle was determined at random within the possible range. After each motion step with a probability of 10% each circle could with equal probabilities either increase or decrease its horizontal or vertical speed by 1 pixel. If this change would have resulted in a speed outside the range, speed changed into the opposite direction instead. Circles bounced of the boarders of the bounding box in a right angle (also on these motion steps, speed and therefore direction could additionally change with the 10% probability). Circles did not bounce off of each other, that is, a short occlusion was possible.

Design and procedure

Participants performed a multiple object tracking task. They had to press the space bar to initialize each trial. At the beginning of each trial, all circles were displayed stationary for 2000 ms. Three circles were indicated as targets by changing their color from black to white several times. The remaining circles were the distractors. All circles, now indistinguishable, subsequently moved for 6000 ms. After this, the circles stopped moving and subjects had to indicate the three targets by selecting them with the aid of a computer mouse. Subjects were allowed to revise their answer. After participants had chosen three circles they were allowed to proceed. Subjects then received feedback about their tracking accuracy. Correctly chosen targets changed their color to green, erroneously selected distractors became red. At the end of each trial participants received feedback about their performance in the current trial, the number of points collected since the last break and the points collected over the whole training period (see below for details on points).

Participants performed ten training sessions over a period of 14 days; training sessions were scheduled each day except on weekends. Each training session lasted about half an hour, leading to five hours of training in total. A single training session consisted of ten blocks; each block consisted of 10 trials, leading to a total of 100 trials per session. In the case that at the end of the six seconds motion time a target overlapped more than half of its size with another circle, this trial was tagged as invalid, excluded from further analysis and immediately replaced by an additional trial. Only valid trials were analyzed. Participants were not aware of this replacement-procedure. After the last training session, each participant had performed 1000 valid trials in total.

The difficulty of the task was designed to adapt to the performance of participants. All participants started their first training session at level one with three targets and four distractors. If a participant correctly chose at least 27 out of the 30 targets (this corresponds to an accuracy of at least .9) in each of two (not necessarily consecutive) blocks within a single session, he or she proceeded to the next difficulty level. Before the next block started, the participant was informed about having reached the next level. An additional distractor was added on each new level, leading to five distractors in the second level, six distractors in the third, and so on. If a participant correctly chose only 20 out of 30 targets (this corresponds to an accuracy not exceeding .67) in each of four (not necessarily consecutive) blocks within a single session, he or she would return to the preceding difficulty level. However, only two participants fell back, indicating that the learning algorithm was suitable.

Participants gained points as in a video game as an incentive. They were informed that they were paid according to the total points gained during training. These points were calculated as the number of distractors by 10 per correctly clicked target (for example: 4 distractors * 10 = 40 points per correctly clicked target), leading to 40 points per correctly clicked target in level one, 50 points in level two and so on. At the end of the training, they were paid according to their total points. Participants earned between 40 and 81 € for the training. By means of this monetary incentive and the possibility to gain more points in higher levels, we endeavored to incentivize participants to improve their tracking performance. To further motivate them, a personal high score was calculated as the maximum number of points earned within two consecutive blocks.

9.3 Results

Data were analyzed by analysis of variance (ANOVA) or one-tailed *t*-tests. If the ANOVA-results were corrected for non-sphericity using the Greenhouse-Geisser-correction (Greenhouse & Geisser, 1959), we report Greenhouse-Geisser epsilons (ε) and corrected *p*-values (p_{corr}) together with the original *F*-values and original degrees of freedom. One-tailed *t*-tests were employed to test for differences between two values in the predicted direction.

In all graphs, 95%-confidence intervals are calculated according to the procedure described by Jarmasz and Hollands (2009) and are based on the error term of the respective effect of interest. We corrected the critical effects' *df*s appropriately if εs were too low, as suggested by Loftus and Masson (1994). The effects on which the confidence intervals are based on can be found below each figure.

9.3.1 Training

The training improvement over the 10 training sessions is depicted in Figure 9.2. Shown is the maximum number of distractors per session averaged over participants. The mean number of maximally handled distractors spans from 6.85 (range: 5-8) distractors in session one to 10.80 (range: 8-15) distractors in session ten. An analysis of variance yielded a significant main effect of session, $F(9,171) = 75.69$, $\varepsilon = .36$, $p_{corr} < .001$, $\eta^2_{partial} = .80$.

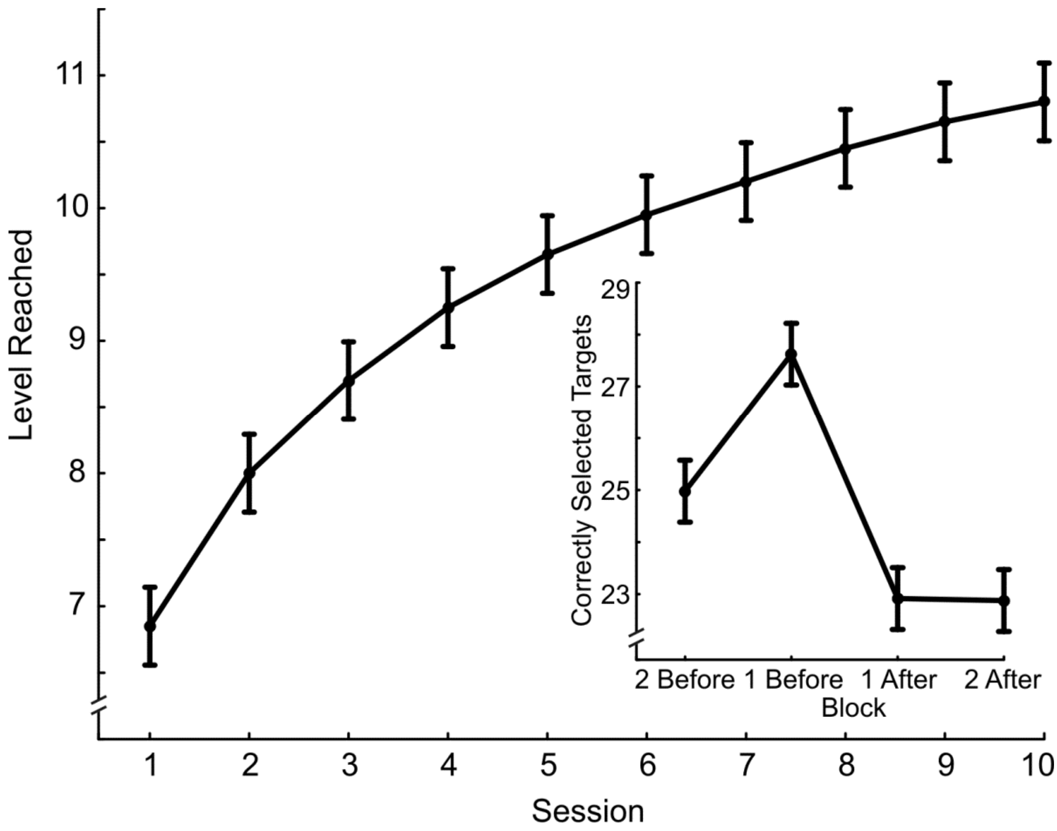

Figure 9.2. Training curve of the multiple object tracking training over all ten training sessions and an illustration of the drop of performance after reaching a new level. The smaller graph displays the mean number of correctly selected (from a total of 30) targets in the two blocks before and after reaching a new level. The displayed 95%-confidence intervals are based on the effect of session or block, respectively.

To test for the predicted drop in performance at the beginning of each new level, we conducted an ANOVA on tracking accuracies in the two blocks before and the two blocks after a new level was reached. Data from the first session were excluded from this analysis, because for some participants the first levels were not challenging enough, as indicated by ceiling effects. We found a significant main effect of block, $F(3,57) = 57.53$, $\varepsilon = .82$, $p_{\text{corr}} < .001$, $\eta^2_{\text{partial}} = .75$. Tracking accuracies in either of the last two blocks before a new level was reached were significantly higher than tracking accuracies in either of the first two blocks in the new level, all four $F(1,19)$s > 16.56, all ps < .001.

9.3.2 Pre- and post-training session

To analyze participants' filter ability, we conducted three comparisons, each of which includes a low- load, a high-load and a distractor-present condition. Comparison 1: 2T, 4T and 2T2D, Comparison 2: 2T, 5T and 2T3D and Comparison 3: 3T, 5T, 3T2D. As the critical results for all three comparisons are the same, in the following we focus on Comparison 1 in order to keep the results section concise. Mean values and 95%-confidence intervals for Comparison 2 and 3 are only shown in Table 9.1, but are not further analyzed.

Behavioral data.

The mean performance accuracy for all conditions of Comparison 1 is shown in Table 9.1. Performance declined with an increasing number of targets and also when irrelevant distractors were added. Performance in the distractor-present condition (2T2D) was between that of 2T and 4T. Furthermore, performance was higher during the post-training session as compared to the pre-training session. A 3 (number of items) × 2 (group) × 2 (session)-ANOVA on mean accuracies confirmed an effect of the number of items, $F(2,76) = 148.62$, $\varepsilon = .81$, $p_{corr} < .001$, $\eta^2_{partial} = .80$. Performance was worse for 2T2D than for 2T, $F(1,38) = 18.14$, $p < .001$ and for 4T than for 2T2D, $F(1,38) = 182.39$, $p < .001$. The effect of session was significant, $F(1,38) = 5.33$, $p < .05$, $\eta^2_{partial} = .12$, with accuracy being higher in the post-training as compared to the pre-training session. There was no effect of group, nor any two-way interaction including group, all ps > .41. The three-way interaction was not significant either, $F(2,76) = 2.50$, $\varepsilon = .84$, $p_{corr} = .10$, $\eta^2_{partial} = .06$. Comparing mean accuracies from pre- and post-training session indicated high retest-reliability, $r_{tt} = .79$.

We calculated a measure of filtering efficiency for each participant and for each session, by subtracting response accuracy for 2T2D from accuracy for 2T. In these two conditions the same number of targets has to be maintained. The better participants are able to filter out the irrelevant distractors in the 2T2D condition, the more the resulting accuracy pattern approaches that of the pure-target condition (2T). Low values indicate high filtering ability whereas high values indicate low filtering ability. Overall accuracy in the pre- and post-training session correlated with this measure of filter ability in both, the pre- and the post-training session, all four rs < -.53, all ps < .001. The same was true for mean accuracy for conditions 2T, 3T, 4T and 5T (conditions without filter affordances), all four rs < -.43, all ps < .01. This data reflects a strong relationship between WM capacity and filter ability.

There was no transfer effect to fluid intelligence, as indicated by the lack of an group by session interaction on Advanced Progressive Matrices scores, $F(1,38) = 0.15$, $p = .71$ and therefore these data are not further discussed.

Table 9.1

Mean Accuracies, Mean Contralateral Slow Potential Amplitudes and Mean CDA Amplitudes with the Respective 95% Confidence Intervals (CI) as a Function of Number of Items, Group and Session

	Number of Items							95% CI		
Condition	2T	3T	4T	5T	2T2D	2T3D	3T2D	C1	C2	C3
Accuracies										
Training										
Pre	.97	.91	.84	.77	.94	.91	.86			
Post	.97	.92	.85	.79	.95	.94	.89			
Control								±.01	±.02	±.02
Pre	.97	.91	.87	.80	.94	.90	.87			
Post	.98	.93	.86	.78	.97	.94	.89			
Contralateral Slow Potentials										
Training										
Pre	-4.67	-5.53	-6.03	-6.21	-5.41	-5.56	-5.92			
Post	-5.01	-6.11	-6.66	-6.62	-5.41	-5.73	-6.06			
Control								±0.34	±0.37	±0.32
Pre	-5.34	-6.49	-7.09	-7.58	-6.48	-6.88	-7.40			
Post	-5.75	-6.53	-7.81	-7.68	-6.36	-7.17	-7.38			
CDA										
Training										
Pre	0.08	-0.38	-0.62	-0.51	-0.55	-0.63	-0.74			
Post	0.59	-0.10	-0.45	-0.22	-0.44	-0.39	-0.66	±0.22	±0.22	±0.21
Control										
Pre	0.25	-0.55	-0.62	-0.77	-0.90	-0.92	-0.98			
Post	-0.04	-0.34	-0.76	-0.66	-0.71	-0.95	-1.02			

Note. CIs are calculated separately for the three comparisons according to the procedure suggested by Jarmasz and Hollands (2009) for the interpretation of the Number of Items × Session-interaction within each Group. T = targets; D = distractors; C = Comparison (see text for details); Training = training group; Control = control group; Pre = pre-training session; Post = post-training session.

ERP data

Analyses were based on mean voltage amplitudes averaged over the time window from 320 to 700 ms after the onset of the memory array. As anticipated, the number of relevant items had the strongest effect on activity measured over electrodes at posterior recording sites, especially at PO3/4. We consequently analyzed CDA and contralateral slow potential amplitudes at this electrode site. Effects on CDA and contralateral slow potential amplitudes were analyzed separately by two 3 (number of items) × 2 (group) × 2 (session)-ANOVAs. We observed a very high retest-reliability for the mean amplitudes of CDA and contralateral slow potentials averaged over all conditions, $r_{tt} = .80$ and $r_{tt} = .92$, respectively.

The CDA amplitude as a function of number of items, session and group is shown in Figure 9.3. An ANOVA on the mean amplitude of the CDA revealed a significant main effect of number of items, $F(2,76) = 61.31$, $\varepsilon = .88$, $p_{corr} < .001$, $\eta^2_{partial} = .62$, and a significant Number of Items × Group × Session-interaction, $F(2,76) = 4.18$, $\varepsilon = .98$, $p < .05$, $\eta^2_{partial} = .10$. This interaction was not, however, driven by more efficient filtering by the training group in the post-training session. As can be seen in Figure 11.3, the mean amplitudes for 2T2D were never lower than the amplitudes for 4T; the difference in amplitude for the control group in the pre-training session between 2T2D and 4T was marginally significant into the unexpected direction, $F(1,38) = 3.07$, $p = .09$; all other $F(1,38)$s < 0.19, all ps $> .66$. This pattern would indicate no filtering in either session. Amplitudes for 2T, in contrast, were always lower than for the other two conditions, all $F(1,38)$s > 10.82, all ps $< .003$.

The amplitudes of the contralateral slow potentials as a function of number of items, session and group are shown in Figure 11.4. An ANOVA on the mean amplitudes of the slow potentials revealed a significant main effect of number of items, $F(2,76) = 44.42$, $\varepsilon = .90$, $p < .001$, $\eta^2_{partial} = .54$, and a significant interaction between number of items and session, $F(2,76) = 4.65$, $\varepsilon = .90$, $p < .05$, $\eta^2_{partial} = .11$. There was neither a main effect nor an interaction for group, all ps $> .43$. The three-way interaction was not significant, either, $F(2,76) = 0.13$.

To sum up, there was no evidence of transfer effects, in terms of a training-induced increase in filter abilities, in the accuracy measures or in the CDA or contralateral slow potentials.

9.3.3 Training effects in change detection—All participants

We did not observe a training induced increase in filter abilities specific for the training group. However, a closer inspection of the data revealed an overall training effect for both groups, as reflected by the interaction between session and number of items in the contralateral slow potentials (see Figure 9.4). In the post-training session, amplitudes for 2T2D are closer to 2T and further afar from 4T than in the pre-training session as to be expected if participants improved their filtering ability. As evident in Figure 9.4, in the post-training session the ERP for 2T2D at about 400 ms fully overlaps with the ERP for 2T, indicating an exclusion of distractors. In an exploratory analysis on the combined data of the training and control group, we confirmed a significant decrease in the difference between 2T and 2T2D and a significant increase of the difference between 4T and 2T2D from the pre- to the post-training session, *t*(39) = 1.75, *p* < .05 and *t*(39) = 3.70, *p* < .001, respectively. Further indicating that the interaction was driven by an increase in filter ability and not visual WM capacity, the difference between 2T and 4T does not significantly change over sessions, *t*(39) = 1.14, *p* = .13.

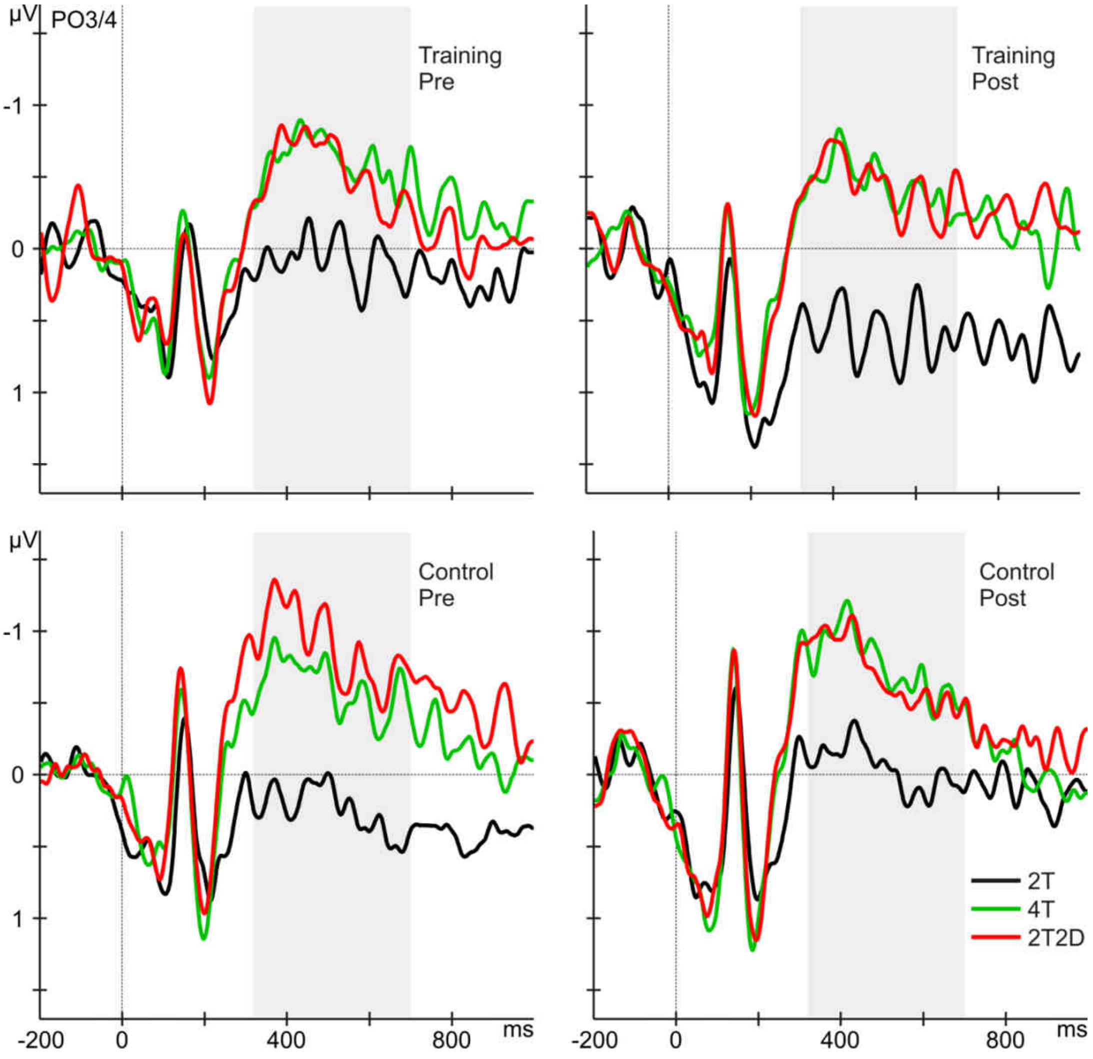

Figure 9.3. Grand averaged CDAs at PO3/4 relative to the onset of the memory array. Colors code the number of items (black, two targets, 2T; green, four targets, 4T; red, two targets and two distractors, 2T2D). The upper two graphs show the training group (train), the lower two graphs the control group (control). The pre training session (pre) is shown on the left, the post training session (post) on the right.

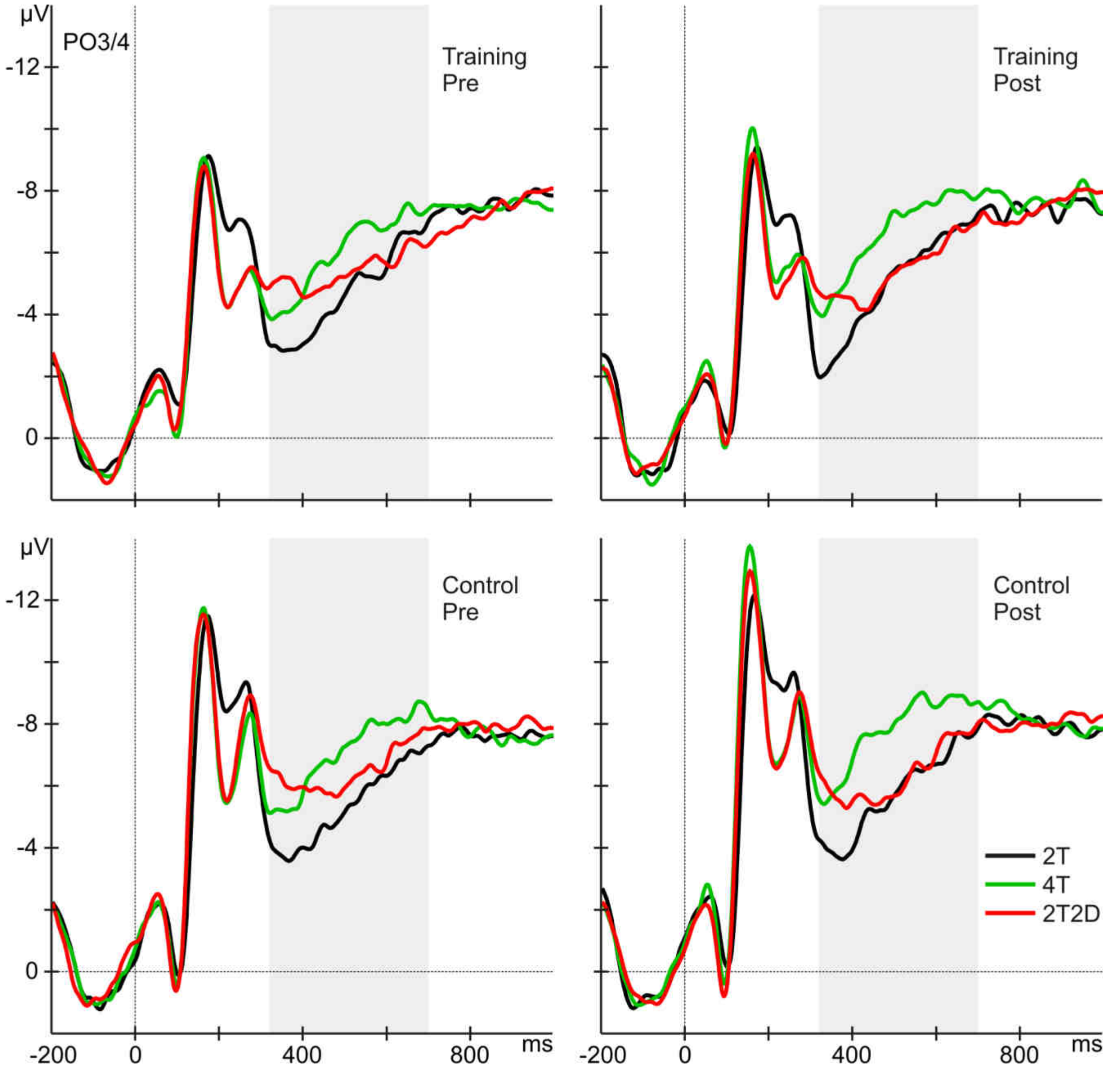

Figure 9.4. Grand averaged contralateral slow potentials at PO3/4 relative to the onset of the memory array. Colors code the number of items (black, two targets, 2T; green, four targets, 4T; red, two targets and two distractors, 2T2D). The upper two graphs show the training group (train), the lower two graphs the control group (control). The pre training session (pre) is shown on the left, the post training session (post) on the right.

Furthermore, the accuracy data confirm the overall training effect. The decrease in the difference between 2T and 2T2D and the increase of the difference between 4T and 2T2D from the pre- to the post-training session were significant, $t(39) = 1.84$, $p < .05$ and $t(39) = 1.85$, $p < .05$, respectively. As for the slow potentials, further confirming an increase in filter ability and not in visual WM capacity, the difference between 2T and 4T does not change over sessions, $t(39) = 0.68$, $p = .25$.

9.4 Interim Discussion

We found (a) a large training gain in the ability to filter out irrelevant distractors in MOT for the experimental group and (b) suggestive evidence for an improvement of the ability to filter out irrelevant distractors in a change detection task for both, training- and control group. However, training filtering ability in MOT did not transfer to improved filter ability in the change detection task with distractors. What can be concluded from these results? Apparently, the filter process in MOT differs from the filter process in the change detection task. We planned a follow-up investigation to reassure that we indeed trained the selection mechanism of allocation of attention in MOT. Firstly, we wanted to exclude the possibility that the training group trained a very specific strategy during MOT, such as for example grouping strategies, only suitable in our particular MOT design. Secondly, we wanted to gain additional evidence that the training group indeed improved their ability to allocate attention.

9.5 Follow-Up Investigation

9.5.1 Introduction

As discussed above, when the number of distractors in MOT increases, filtering requirements are also increased (Bettencourt & Somers, 2009). During an adaptive MOT training, we exclusively manipulated the number of distractors. Each time participants reached a specified threshold, they advanced to a higher level in which a further distractor was added. Applying this specific training design, we aimed to specifically train participants' ability to filter out irrelevant distractors. The observed accuracy pattern supports our hypothesis that participants indeed improved their selection mechanisms. (a) The training group showed large training gains in MOT. Over the training sessions they learned to deal with a larger number of distractors. (b) Each time participants advanced to a higher level their accuracy typically dropped again (see Figure 9.2). This initial drop in accuracy probably reflects the difficulty of handling an increased number of distractors. Although the observed data pattern clearly indicates an improvement of the training group's selection mechanisms, we aimed to further support this interpretation and collect converging evidence.

An often discussed alternative learning mechanism in MOT tasks is the development of grouping strategies. For example, Yantis (1992) reports a performance improvement after instructing participants to use a grouping-to-shape strategy in a MOT task. This strategy comprises the mental formation of a virtual shape out of the to-be-tracked targets, with the tracked targets being the corners of this mental shape. In this way, participants tracked one single object, constantly moving in space and changing its shape. As they always had to track three targets, our participants might have discovered the strategy to build up and track a virtual triangle. However, the sudden drop in performance each time participants advanced to a new level constitutes evidence against such an explanation. It is difficult to see how applying a strategy of tracking a virtual triangle could lead to such a drop in performance when a single new distractor was added. Although we feel confident that the observed performance improvements during the MOT training reflect improved selection mechanisms, we aimed to exclude the alternative explanation that the training group learnt any specific strategy for tracking exactly three targets such as the triangle-strategy. We therefore tested whether participants of the training group improved their general ability to keep track of moving objects and therefore show a transfer to tracking four objects. Please note that due to improved performance to track three targets, participants of the training group could achieve a higher overall accuracy score than participants of the control group in this task without having any real transfer effects to the ability to track four targets. If three targets is already close to a participant's tracking limit, an attempt to track four targets might overload this participant's abilities. For this participant it might pay off to continue to track three out of the four targets. Such a pattern might lead to a higher overall accuracy score for the training group even if they only learned to track three targets. To gain a hard proof of a transfer to tracking four targets, we counted only those trials as correctly solved, in which participants reported all four targets correctly.

One technique valuable to gain insights into the exact nature of the attentional processes running during the MOT task is the dot probe technique (e.g., Doran & Hoffman, 2010; Drew et al., 2009; Pylyshyn, 2006). While participants perform a MOT main task, they additionally have to detect a small, shortly appearing dot as a secondary task. The dots appear either on target positions, distractor positions or in the empty space in between the moving objects. From participants' ability to detect this dot inferences can be drawn concerning their allocation of spatial attention in the display at a specific point in time. At locations in the display where attention is currently focused, detection of shortly appearing dots should be strongly improved. Applying this technique, we searched for additional evidence that the training group improved the process of attention allocation during MOT training. The hypothesized training of attention allocation might become evident in two directions. The filtering our participants learned might either consist in a suppression of distractors or in an enhancement of targets or both. If the control group outperformed the training group in detecting dots at distractor locations, this would indicate that participants of the training group had learned to inhibit the distractors. If the training group outperformed the control group in detecting dots at target locations, this would indicate that participants of the training group had learned to attentionally enhance the targets.

As the training and the follow-up investigation were separated by at least seven months, we initially tested whether training effects still persisted. If the training was long-lasting in nature, the training group should outperform the control group in the MOT task with three targets that they had performed during training.

9.5.2 Methods

Participants

All 40 participants of the training study were invited to participate in a follow-up investigation. As the follow-up study was initiated seven months after the training study, only 29 of the originally 40 participants were available for participation in the follow-up study (2 left-handed, mean age: 26.10 years, range: 20-34, 21 female, 16 from the training group).

Stimuli

Moving circles were the same as in the training task. The dot probe was a red dot, with a diameter of 0.13° of visual angle in size.

Design and procedure

Participants attended two testing sessions which were separated by about one week. In both sessions, participants performed the MOT task. The trial procedure was the same as in the training sessions. We also applied the same procedure of replacing invalid trials.

In the first session, we ran five blocks of the MOT task (non-adaptive); each block comprised of 20 valid trials. The first three blocks were designed to test for long lasting training effects. In these three blocks participants tracked three targets. There were six distractors in the first (3T6D), eight in the second (3T8D) and eleven in the last (3T11D) of these three blocks. The last two blocks were designed to test transfer effects. They consisted of four targets and six distractors in the first (4T6D) and eight distractors in the second block (4T8D).

In the second session, participants performed the MOT task (non-adaptive) together with a concurrent dot probe task. Participants performed 240 valid trials. On each trial, participants tracked three targets among eight distractors. While the circles were moving, in half of the trials a little red dot appeared for 120 ms with an equal probability of one third at one of three possible types of locations: at a target, at a distractor or in the empty space in between (within the defined invisible rectangle, see Chapter 9.2.3). If the dot was placed on a target or distractor it moved along with the respective circle for the 120 ms of its appearance. After tracking, participants solved two tasks. Their first task was to identify the three targets out of the eight distractors (see Chapter 9.2.3 for the exact procedure). After this decision, they indicated by key-press whether a red dot had appeared or not during this trial. Key assignment was counterbalanced.

9.5.3 Results

Data were analyzed as described above.

Due to software problems, the experiment was terminated during the last block of session one (4T8D) for one subject. As we had to remove data from the last block for this subject and therefore had a different number of subjects for the conditions 4T6D and 4T8D, the transfer-effects were tested for the predicted order (training group > control group) by 2 one-tailed t-tests.

The analysis of long-lasting training effects was based on the percentage of correctly tracked targets. One participant performed only 18 out of 20 valid trials in block two (3T8D). A 3 (number of distractors) × 2 (group)-ANOVA yielded an effect of the number of distractors, $F(2,54) = 103.14$, $\varepsilon = .92$, $p < .001$, $\eta^2_{\text{partial}} = .79$, and an effect of group, $F(1,27) = 5.19$, $p < .05$, $\eta^2_{\text{partial}} = .16$. The interaction was not significant, $F(2,54) = 0.01$. Participants of the training group (mean percentage correct = .80, SD = .06) outperformed participants of the control group (mean percentage correct = .74, SD = .09) in their tracking performance.

To test for transfer-effects, analyses were based on the number of trials in which all four targets were correctly tracked. In contrast to the other MOT analyses and as explained above, participants received one or zero points per trial, depending on whether they correctly tracked all 4 targets or not. The training group outperformed the control group in tracking four targets in both, 4T6D and 4T8D, $t(27) = 1.51$, $p = .07$ and $t(26) = 2.07$, $p < .05$, respectively.

Concerning the data of the second follow-up session, we analyzed the percentage of correctly tracked targets to test for long lasting training effects and the percentage of detected dots to test for differences in attention allocation between training and control group.

The training group had higher tracking performance accuracy than the control group, $t(27) = 1.95$, $p < .05$. This result further supports our findings of long lasting training effects of the training group, as reported above.

A 3 (dot location) × 2 (group)-ANOVA on mean dot detection accuracy yielded a significant main effect of dot location, $F(2,54) = 60.95$, $\varepsilon = .72$, $p_{\mathrm{corr}} < .001$, $\eta^2_{\mathrm{partial}} = .69$, and a marginally significant interaction, $F(2,54) = 3.20$, $\varepsilon = .72$, $p_{\mathrm{corr}} = .07$, $\eta^2_{\mathrm{partial}} = .11$, but no effect of group, $F(1,27) = 2.71$, $p = .11$, $\eta^2_{\mathrm{partial}} = .09$. Deconstructing the interaction, there was a group effect for dot detection accuracy if dots had appeared on distractors, $F(1,27) = 6.70$, $p < .05$, but not if dots had appeared on targets or in empty space, $F(1,27) = 2.30$, $p = .14$ and $F(1,27) = 0.02$, $p = .88$, respectively. The training group was worse than the control group in detecting dots on distractor locations.

Participants in the control group might have allocated more resources to the detection of dots and less resources to tracking the targets as compared to the training group. We were able to test this alternative interpretation, as we had run a block with three targets and eight distractors also in the first session of the follow-up study. If, in the second session of the follow-up study, participants of the control group traded their tracking performance off for a higher dot detection rate, they should show a lower tracking performance as compared to the first session of the follow-up study. This would predict a 2 (session) x 2 (group)-interaction, which was not significant, $F(1,27) = 0.07$. This implies that there was no reduction in the control group's concentration on tracking the targets in the MOT task in the second session.

9.6 Discussion

We were interested in the plasticity of selection mechanisms in visual WM, because the ability to filter out irrelevant distractors and to focus on relevant information is crucial for successful visual WM performance. We aimed to train participants' selection mechanisms through MOT training, as this task puts heavy demands on participants' filter ability. The selection mechanism that both the MOT task and the change detection task with distractors rely upon, is the selective allocation of attention (Bettencourt & Somers, 2009; Drew et al., 2009; Fukuda & Vogel, 2009; Pylyshyn, 2006; Pylyshyn et al., 2008). As such a partial overlap of processes is considered to be crucial for successful transfer (Dahlin et al., 2008; Jaeggi et al., 2008; Jonides, 2004), we hypothesized that the training of filtering ability in MOT should transfer to improved filter ability in a change detection task with distractors. We observed large training gains in filtering ability in the MOT task. Moreover, we found suggestive evidence that filter ability (from the pre- to the post-training session) also improved in the change detection task with distractors for both the training and the control group. However, although selection mechanisms were shown to be improvable through training in both tasks, we did not observe a transfer from filter training in MOT to improved filter ability in the change detection task with distractors.

Participants in the training group underwent a well-controlled adaptive two-week MOT training program specifically tailored to improve their selection mechanisms. During our MOT training, we increased the number of distractors depending on the progress participants had made. We collected converging evidence, from the training study and a follow-up study, that participants indeed trained their filter ability in terms of attention allocation. The accuracy pattern of the MOT training already indicated that participants had trained their filter mechanisms. Firstly, the training group showed a clear training gain over sessions. They improved their selection mechanisms as evident by the increasing number of successfully ignored distractors. Secondly, the typical pattern, when a new distractor was added during training, was that participants' performance initially dropped down but recovered over time. This indicates that increasing the number of distractors made the task more difficult. Over time, participants learned to handle the increasing number of distractors, which means they learned to improve their selection mechanisms. Additionally, data collected during a follow-up study allowed us to exclude alternative explanations and provided further evidence for the interpretation that the training group had trained their selection mechanisms in terms of attention allocation. Firstly, the training group outperformed the control group in tracking four targets, although tracking four targets had not been trained. We can thus exclude the possibility that the training group only trained some very specific form of strategy which works for tracking exactly three targets only, such as tracking a virtual, moving triangle whose corners are defined through the targets. Secondly, with the aid of the dot probe technique we were able to gain even more direct evidence that participants of the training group had improved their selection mechanisms during the MOT training. The dot probe technique allows measuring the allocation of attention in the display at a specific time point. Detection of briefly presented dots is strongly improved if attention focuses on the given spot at the time of appearance. Employing this technique, we were able to gain further insights into the nature of the trained selection mechanisms. Participants of the control group outperformed participants of the training group in detecting dots at distractor locations, indicating that the control group was less able to ignore irrelevant distractors.

Although evidence that performance in the MOT task is improvable already exist (Allen et al., 2004; Barker et al., 2010; Green & Bavelier, 2006; Pylyshyn, 2006), to our knowledge, this is the first time that a sample of subjects systematically trained the MOT task. Furthermore, the observed object tracking-training effect proved to be very stable and long-lasting. Even months after training, the training group outperformed the control group in their tracking performance, as indicated in a follow-up study. MOT is relevant in a wide field of applications, such as aviation control, but also in daily life, for example in road traffic or when taking care on a group of children moving around, etc. Successful training thus gains importance beyond the scope of this article.

Despite these considerable improvements in filter ability in MOT, we did not observe a transfer to improved selection mechanisms in the change detection task with distractors. However, one practice session on a change detection task with filter demands (the pre-training session) apparently already caused a training gain in filter ability for the training as well as the control group. This increase in filter ability from pre- to post-training session was evident in the accuracy as well as the contralateral slow potential data. This training gain was specific to filter ability, as indicated by the performance improvement in the distractor-present conditions as compared to the pure-target conditions. Interestingly, one training session was obviously not sufficient to increase visual WM capacity. However, this short training was apparently already sufficient to induce increased filter ability. This indicates that a training of filter ability is more efficient than a training of visual WM capacity proper. Further and more direct testing would be desirable to gain converging evidence for the efficiency of training filter ability in a visual WM task.

As the amplitudes of contralateral slow potentials and the CDA vary as a function of visual WM load (Ikkai et al., 2010; Lehnert & Zimmer, 2008; Mecklinger & Pfeiffer, 1996; Rämä et al., 1997; Robitaille, et al., 2009; Robitaille et al., 2010; Ruchkin et al., 1995; Ruchkin et al., 1992; Vogel & Machizawa, 2004; Vogel et al., 2005), they are interpreted as mirroring the maintenance of information in visual WM. In the current study, however, we observed a discrepancy between the pattern of CDA and contralateral slow potentials. The similarity of CDA amplitudes in distractor-present conditions and the respective high-load conditions suggest that the distractors were not filtered out (4T = 2T2D). Contralateral slow potential amplitudes, however, were lower for the distractor-present conditions as compared to the respective high-load conditions, indicating that the distractors were filtered out to a certain degree in distractor-present conditions (4T > 2T2D). The contralateral slow potential pattern is more in line with the observed accuracy data. In addition, the improved filter ability in the change detection task with distractors from pre- to post-training session for both groups is reflected in the accuracy as well as the contralateral slow potential pattern. In line with the claim that contralateral slow potentials mirror the maintenance of information held in visual WM, their amplitudes have been shown to be a function of memory load (Lehnert & Zimmer, 2008; Mecklinger & Pfeiffer, 1996; Rämä et al., 1997; Ruchkin et al., 1995; Ruchkin et al., 1992). However, task difficulty, arousal and the amount of effort might also increase with the number of items and might therefore be confounded with memory load

(McCollough et al., 2007; Vogel & Machizawa, 2004). Consequently, the amplitude modulation of slow potentials can also partly be explained by these factors. The CDA in contrast is corrected for such influences and therefore is considered a pure measure of the number of items held in visual WM, with their amplitude being influenced only by the number of items actually held in visual WM (McCollough et al., 2007; Vogel & Machizawa, 2004). Apparently, slow potentials and CDA reflect partly different aspects of visual WM performance. Based on the present knowledge a definite conclusion on the exact processes underlying these components cannot be drawn. However, both components seem to be related to maintaining visual information in WM.

We report a correlation between visual WM capacity and filter ability in the change detection task. There is plenty of data showing a close link between WM capacity and filter ability. Persons with high WM capacity seem to have better selection mechanisms that regulate access to WM (Engle et al., 1999; Fukuda & Vogel, 2009; Vogel et al., 2005). It seems plausible, that the ability to prevent unnecessary storage is an important determinant for WM capacity for relevant information.

Our results lead to three important conclusions. Firstly, we collected converging evidence that our MOT training indeed improved participants' filter ability. In addition, we found suggestive evidence for an overall improvement in filter ability in the change detection task with distractors. To our knowledge, this is the first study showing that selection mechanisms can be specifically trained. This result has important implications, because selection mechanisms are considered to be of importance for limiting access to WM and therefore for protecting memory resources from overload (Awh & Vogel, 2008). Furthermore, allocation of attention is considered to be the crucial link between WM performance and general intelligence (Heitz, Unsworth & Engle, 2005). Consequently, our finding that selection mechanisms are specifically trainable has implications beyond the topic and the tasks of the present article.

Secondly, filter ability appears to be trainable in both tasks, but improved filter ability in MOT did not transfer to the change detection task with distractors. This indicates that, in contrast to our initial hypothesis, the process of selection might not be the specific process in which both tasks primarily overlap. The close relationship between the two tasks as discussed in detail above might be due to sharing a common WM store or, in other words, common WM maintenance processes. A possible neural source underlying this process might be the intraparietal sulcus (IPS) as activity in the IPS increases with increasing load in the MOT as well as the change detection task (Culham, Cavanagh & Kanwisher, 1998; Jovicich et al., 2001; Todd & Marois, 2005; Xu & Chun, 2006). The IPS might work as a pointer-system that can maintain a highly limited number of objects active in the retention period of a visual WM task and during tracking of multiple objects (Drew & Vogel, 2008).

Thirdly, the selection mechanism in the MOT as well as the change detection task with distractors is considered to be attention allocation (Bettencourt & Somers, 2009; Drew et al., 2009; Fukuda & Vogel, 2009; Pylyshyn, 2006; Pylyshyn et al., 2008). Our results, however, indicate that even a mechanism that seems that accurately defined needs to be further differentiated. With the aid of the MOT task we successfully trained the ability to sustain selective attention on targets. A critical difference might be the available time for target selection. During MOT there is enough encoding time to differentiate between targets and distractors and to allocate attention towards the targets. Filtering then consists in actively suppressing distractors over several seconds. In the change detection task by contrast, stimuli are presented for a very short time (100 ms). The filtering bottleneck might therefore be the discrimination of targets and distractors during encoding. Although selection mechanisms in both tasks are object-based (Pylyshyn, 2006), they actually have slightly different demands on attention allocation in space and over time.

Our results indicate that allocation towards the targets and prevention of attentional capture through distractors is not the crucial selection mechanisms in the change detection task with distractors as employed in the present study. In the General Discussion, we will therefore reconsider the attentional processes during selection in change detection tasks and discuss further possible selection mechanisms.

Part 4

Beyond the Scope of the Training Question

10 Further Inferences from the Training Data

In Experiment 3 we collected a fair quantity of data and analyzed them with the focus on plasticity of selection mechanisms. Among others, participants performed the lateralized change detection task with distractors. To explore training effects, participants were divided into two groups (training and control group). At the time of the pre training session training and control group did not differ. Consequently, for the pre training data, all participants can be combined into one large subject sample. This is a welcome opportunity to exceed the "boundaries" of the original research question and analyze visual WM processes for a large sample (40 participants). Based on hypotheses drawn from the existing literature and previous experiments (Experiment 1 and 2), in the following, we analyze three further issues.

Please refer to the methods part of Experiment 3 (Chapter 9.2.2) for any information concerning the tasks or electrophysiological recordings.

All data in the following three chapters were analyzed by analysis of variance (ANOVA). If the ANOVA-results were corrected for non-sphericity using the Greenhouse-Geisser-correction (Greenhouse & Geisser, 1959), we report Greenhouse-Geisser epsilons (ε) and corrected p-values (p_{corr}) together with the original F-values and original degrees of freedom. Effects and interactions were further decomposed by contrasts.

In all graphs, 95%-confidence intervals are calculated according to the procedure described by Jarmasz and Hollands (2009) and are based on the error term of the respective effect of interest. We corrected the critical effects' *df*s appropriately if εs were too low, as suggested by Loftus and Masson (1994). The effects on which the confidence intervals are based can be found below each figure.

11 The Contribution of Ipsilateral Delay Activity

As the ipsilateral slow potentials did not add any interesting aspect to the training questions (no training related changes in activity) and we had to keep analyses condensed, with a clear focus on training-related questions, we decided not to report the ipsilateral activity within the scope of the training question (see Experiment 3). However, one of the main research questions of the first part of this work—Experiments 1 and 2—was the characterization of ipsilateral delay activity in the lateralized change detection task. The appearance of ipsilateral slow potential amplitudes as a function of visual WM load varied between Experiment 1 and 2. In Experiment 1, set size manipulations resulted in corresponding modulations of ipsilateral delay activity. Contrary, in Experiment 2, there was no set size-dependent ipsilateral delay activity if more than one relevant item was presented. In order to gain further hints regarding the behavior of ipsilateral delay activity, we analyzed this activity in the data from the lateralized change detection task of Experiment 3. Although the design of the experiment contains distractor-present trials intermixed with pure-target trials, an analysis of the pure-target trials only (set sizes 2, 3, 4, and 5) constitutes a good occasion to verify the stability of the data of Experiment 1 (set sizes 2, 3, 4, 5, and 6). Based on the results of Experiment 1, we expect to observe again load-dependent amplitude modulations in the ipsilateral slow potentials.

11.1 Results

In the analysis of the training effects we analyzed electrode PO3/4, whereas in Experiment 1 and 2 analyses were based on a pooling of posterior electrodes P3/4, P5/6, P7/8, PO3/4, and

PO7/8. To ensure a better comparability of the present analysis with Experiment 1 and 2, we decided to employ the same pooling here. As in the training study, analyses were based on mean voltage amplitudes averaged over the time window from 320 to 700 ms after the onset of the memory array. Behavioral effects and effects on CDA amplitudes were analyzed by an ANOVA for the number of items (2, 3, 4, or 5 items), and slow potential amplitudes were analyzed by an ANOVA for the number of items (2, 3, 4, or 5 items) and hemisphere (contralateral vs. ipsilateral hemisphere with respect to the relevant hemifield).

A 4 (number of items)-ANOVA on mean accuracies yielded a significant effect of set size, $F(3,117) = 164.59$, $\varepsilon = .70$, $p_{\mathrm{corr}} < .001$, $\eta^2_{\mathrm{partial}} = .81$. All pairwise comparisons were significant, all *F*s > 62.00, all *ps* < .001 (means: 2T = .97; 3T = .91; 4T = .85; 5T = .78).

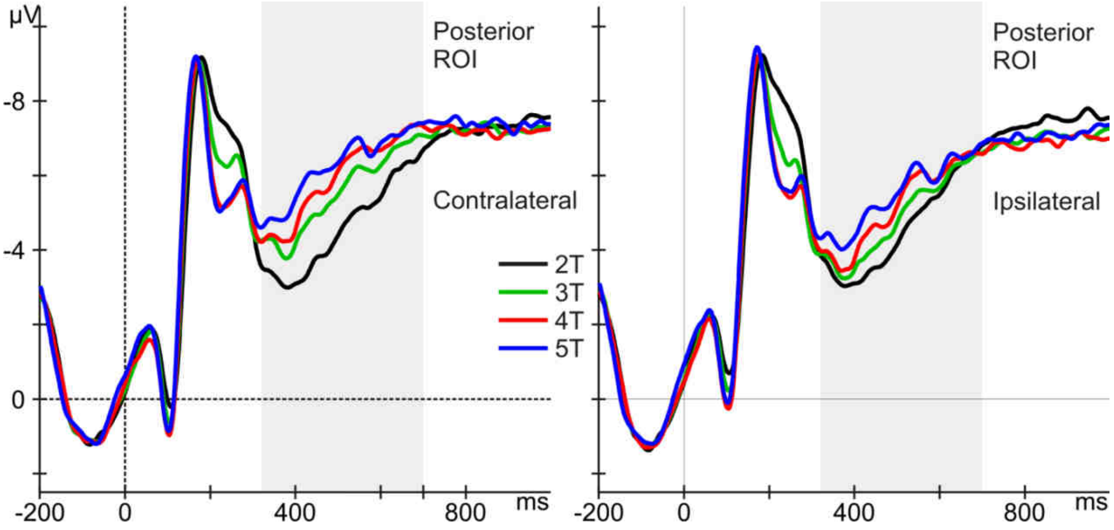

Figure 11.1. Grand averaged contralateral and ipsilateral slow potentials relative to the onset of the memory array at posterior ROI (P3/4, P5/6, P7/8, PO3/4, PO7/8). Colors code the number of relevant items.

As can be seen in Figure 11.1, although, there is set size dependent activity in the contralateral as well as the ipsilateral slow potentials, this effect is stronger for the contralateral as compared to the ipsilateral slow potentials. A 2 (hemisphere) × 4 (number of items)-ANOVA yielded a main effect of hemisphere, $F(1,39) = 8.33$, $p < .01$, $\eta^2_{\mathrm{partial}} = .18$, and a main effect of the number of items, $F(3,117) = 25.73$, $\varepsilon = .79$, $p_{\mathrm{corr}} < .001$, $\eta^2_{\mathrm{partial}} = .40$. These main effects were modulated by a significant interaction between hemisphere and the number of items, $F(3,117) = 19.39$, $\varepsilon = .84$, $p_{\mathrm{corr}} < .001$, $\eta^2_{\mathrm{partial}} = .33$. There was no significant difference between contralateral and ipsilateral slow potentials for set size 2, $F(1,39) = 0.01$, $p = .90$, but for set sizes 3, 4,5, all *F*s > 11.14, all *p*s < .01, confirming the lower load modulations for ipsilateral slow potential amplitudes as evident in Figure 11.2. For contralateral as well as ipsilateral slow potential amplitudes there was a significant load effect from set size two to three and three to four, all *F*s > 4.72, all *p*s < .05. The difference between set sizes 4 and 5 was only marginally significant for contralateral as well as ipsilateral slow potential amplitudes, $F(1,39) = 3.66$, $p = .06$ and $F(1,39) = 3.90$, $p = .06$, respectively.

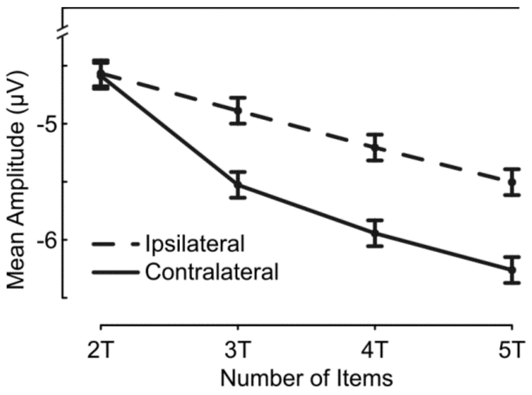

Figure 11.2. Contralateral and ipsilateral slow potentials as a function of the number of items. The displayed 95%-confidence intervals are based on the hemisphere × number of items-interaction.

11.2 Discussion

We exactly replicated the results of Experiment 1. Please refer to Figure 11.3 for a direct comparison of the data patterns of Experiment 1 and the current analysis. Comparable to Experiment 1, in the current analysis amplitudes of the contralateral as well as the ipsilateral slow potentials were modulated by visual WM load. Further replicating the data from Experiment 1, load effects were less pronounced for ipsilateral delay activity as compared to contralateral activity. The exact replication of the data pattern of Experiment 1 constitutes a crucial indication for the stable existence of load-dependent ipsilateral delay activity in the lateralized change detection task. However, the question remains why no load-dependent ipsilateral delay activity was found in the change detection design with imbalanced arrays of Experiment 2. We will discuss the question about the differences between experiments that might have led to the variations in the pattern of ipsilateral delay activity in the General Discussion (see Chapter 16.1).

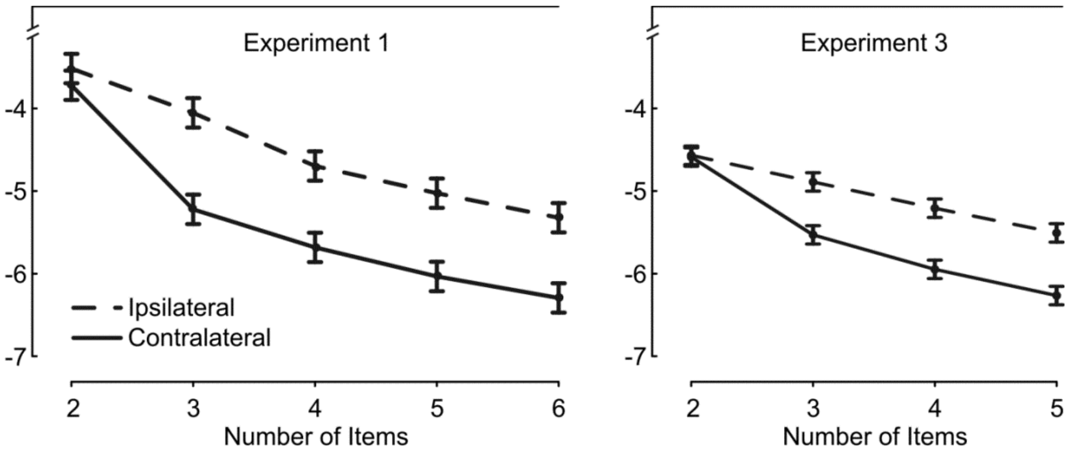

Figure 11.3. Direct comparison of the slow potential pattern of Experiment 1 and the slow potential pattern for the pure target trials of Experiment 3 as a function of hemisphere and the number of items. Please note that these data were already shown above in Figures 5.4 and 11.2, respectively, but are here repeated for your convenience.

12 Explaining the Observed Discrepancies between the CDA and the Contralateral Slow Potentials

As already evident in the training analysis, the filter-patterns of the CDA and the contralateral slow potentials differ (see Chapter 9.3.2). In the pre training session, CDA amplitude for distractor-present conditions equals that of the respective high load conditions (2T2D = 4T), indicating no filtering at all. Contrary, the contralateral slow potential amplitude for distractor-present conditions lies in between the respective high and low-load conditions (2T < 2T2D < 4T; see Figure 9.3 and 9.4), indicating that the distractors were filtered out to a certain degree. This different pattern for CDA and contralateral slow potentials is clear evidence that something interesting is happening in the ipsilateral hemisphere. An analysis of the pattern of ipsilateral delay activity should shed light on the question why contralateral slow potentials and CDA show different filter-patterns.

12.1 Results

As in the training study, analyses were based on mean voltage amplitudes at electrode PO3/4 averaged over the time window from 320 to 700 ms after the onset of the memory array. As in the training analysis we decided to report only results of Comparison 1 (2T, 4T, 2T2D). Effects on CDA amplitudes were analyzed by two ANOVAs of the number of items (2T, 4T, 2T2D), slow potential amplitudes were analyzed by an ANOVAs on the number of items (2T, 4T, 2T2D) and hemisphere (contralateral vs. ipsilateral hemisphere with respect to the relevant hemifield). As we are only interested in electrophysiological data here, we do not report analyses on mean response accuracies. These can however be found below (Chapter 13.1).

As can be seen in Figure 12.1, both contralateral as well as ipsilateral slow potential amplitudes are larger for set size 4T as compared to 2T. In the distractor-present condition (2T2D) contralateral slow potential amplitudes lie in between the two pure-target conditions (2T and 4T), whereas ipsilateral slow potential amplitudes lie at the same level as in condition 2T. A 2 (hemisphere) × 3 (number of items)-ANOVA confirmed the pattern: A main effect of hemisphere, $F(1,39) = 5.23$, $p < .05$, $\eta^2_{\text{partial}} = .12$, and number of items, $F(2,78) = 14.45$, $\varepsilon = .91$, $p_{\text{corr}} < .001$, $\eta^2_{\text{partial}} = .27$, together with an interaction between the two factors, $F(2,78) = 40.26$, $\varepsilon = .99$, $p_{\text{corr}} < .001$, $\eta^2_{\text{partial}} = .51$. Contralateral slow potential amplitudes differed significantly between all three conditions, all Fs > 9.45, all ps < .01. Ipsilateral slow potential amplitudes, however, differed significantly only between 2T vs. 4T and 4T vs. 2T2D, $F(1,39) = 0.89$, p < .001 and $F(1,39) = 12.98$, $p < .001$, respectively, but not between 2T vs. 2T2D, $F(1,39) = .04$, $p = .84$.

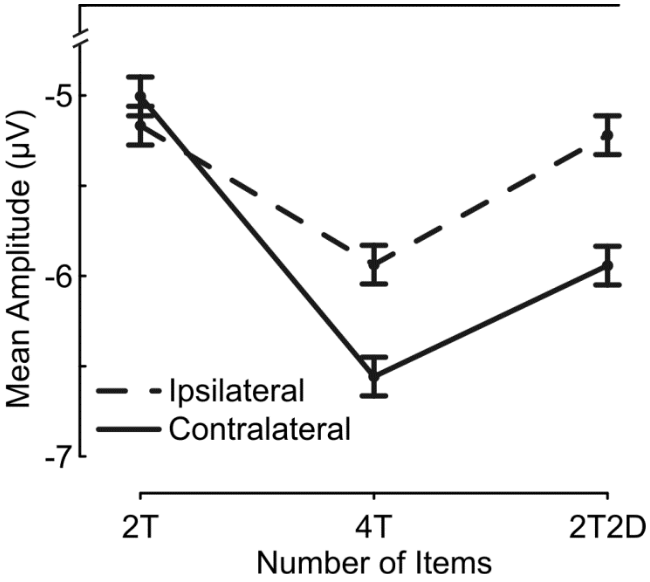

Figure 12.1. Contralateral and ipsilateral slow potentials for Comparison 1. The displayed 95%-confidence intervals are based on the hemisphere × number of items-interaction.

A closer look on Figure 12.1 reveals an interesting pattern. The distance between contralateral and ipsilateral slow potential amplitudes is equal for condition 4T as well as for condition 2T2D. Hence, CDA amplitude must be equal for the two conditions 4T and 2T2D. Indeed, a 3 (number of items)-ANOVA on mean CDA amplitude confirmed the inferences from slow potential analysis: A main effect of the number of items, $F(2,78) = 40.26$, $\varepsilon = .99$, $p_{\text{corr}} < .001$, $\eta^2_{\text{partial}} = .51$, goes back to a significant difference between 2T and 4T as well as 2T and 2T2D, $F(1,39) = 50.93$, $p < .001$ and $F(1,39) = 15.63$, $p < .001$, respectively. The amplitudes in conditions 4T and 2T2D however, do not differ, $F(1,39) = 0.25$, $p = .36$ (see Figure 9.3).

12.2 Discussion

In the training study, we observed a discrepancy in the data pattern of CDA and contralateral slow potentials. Whereas CDA amplitudes suggested no filtering of the distractors, the pattern of the contralateral slow potential amplitudes suggested that the distractors were filtered out to a certain degree. The only logical conclusion for the different patterns of CDA and contralateral slow potentials, was that there was systematic activity in the ipsilateral slow potentials.

The combined consideration of contralateral as well as ipsilateral slow potentials illustrates well the origin of the CDA pattern (see Figure 12.1). Interestingly, the distance between contralateral and ipsilateral slow potentials is equal for conditions 4T and 2T2D. Due to the construction of the CDA as the difference wave between contralateral and ipsilateral slow potentials, this slow potential pattern leads to an equivalent CDA amplitude for conditions 4T and 2T2D. Actually, considering the slow potential pattern, it seems more or less arbitrary that the CDA amplitude does not differ for conditions 4T and 2T2D. Probably by chance, the distance between contralateral and ipsilateral slow potentials was equal in condition 4T and condition 2T2D, leading to the erroneous impression that the pattern of CDA activity reflects that the distractors are not filtered out. Contrary, the assumption that the contralateral slow potentials might truly mirror filter effects, is supported by the congruency of contralateral slow potentials and behavioral data. Both measures imply that distractors are filtered out to a certain degree. However, our conclusion that the CDA pattern might have emerged arbitrarily remains highly speculative and further testing is necessary.

Contrary to the pattern of the contralateral slow potentials, ipsilateral slow potential amplitudes were equal for conditions 2T and 2T2D. However, to date the function of ipsilateral delay activity remains unclear. In the General Discussion we will outline further approaches how to learn about the function of ipsilateral delay activity. Not until then their behavior in filter conditions can be understood. Within this work, we concentrate on contralateral slow potentials as indicator of filtering. They might reflect the processing of the items in the relevant hemifield, that is, the processes we are interested in, in the context of selection mechanisms.

13 Frontal Activity as a Trigger of Selection

Individuals differ in their visual WM capacity (Cowan, 2001; Luck & Vogel, 1997; Vogel & Machizawa, 2004). One popular hypothesis claims that differences in visual WM capacity are actually determined by differences in the ability to resist interference. In other words, all persons possess more or less the same amount of storage capacity, but differ in their ability to control what information enters WM (cf., e.g., Awh & Vogel, 2008; Cowan, 2001; Engle, et al., 1999; Perez & Vogel, 2011; Vogel et al., 2005). This assumption is related to the question of how access to visual WM is regulated. Results of single unit recordings in monkeys assign the prefrontal cortex a crucial role in regulating access to visual WM (e.g., Miller, Erickson & Desimone, 1996; Rainer, Asaad & Miller, 1998). The prefrontal cortex also plays a critical role in control processes in humans (for reviews, see Desimone & Duncan, 1995; Miller & Cohen, 2001). One recently published study employed a change detection task with distractor-present and distractor-absent trials (McNab & Klingberg, 2008). Shortly before the presentation of the memory array, participants were cued whether the ensuing trial would contain only targets (pure-target trial) or additionally distractors (distractor-present trial). Crucially, increased activity in the prefrontal cortex and basal ganglia preceded the distractor-present trials but not the pure-target trials. The strength of this increase in activity was predictive for visual WM capacity. Participants whose activity increase was relatively high also had a high visual WM capacity. Furthermore, activity in the global pallidus, a sub region of the basal ganglia, was predictive for unnecessary storage of distractors in WM. The lower the activity increase for distractor-present as compared to pure-target trials, the more distractor information was unnecessarily stored. The authors interpreted the prefrontal and basal ganglia activity as reflecting gatekeepers to WM that control which information is given access to WM. The observed correlation of prefrontal and basal ganglia activity with visual WM capacity is in line with the idea that interindividual differences in attentional control determine visual WM capacity.

In Vogel et al.’s (2005) version of the lateralized change detection task with distractors, participants had to remember the orientation of the red items and ignore the blue distractor items. The authors observed a significant correlation between filter efficiency, as indicated by the CDA and memory capacity (for a detailed description of their design and results see Chapter 7.1). Interestingly, they consider the prefrontal cortex as a plausible neuronal source that sends a bias signal to determine the relevant information and enable efficient selection. Individual differences in filtering efficiency might be determined by variations of this signal (Vogel et al., 2005; see also Awh & Vogel, 2008 for a combined discussion of the results of Vogel et al., 2005 and McNab & Klingberg, 2008).

Based on Vogel et al.’s (2005) ideas, it appears probable that a bias signal, as observed by McNab and Klingberg (2008), is also present in our version of the change detection task. An electrophysiological equivalent to the prefrontal activity boost in the fMRI-study of McNab and Klingberg (2008) might have emerged in our study. In particular, there might be a boost over frontal recording sites in distractor-present trials as compared to pure-target trials.

Following the same logic as already employed for the analysis of this data set in light of the training question (see Chapter 9.3.2), we here employ contralateral posterior slow potentials to infer whether distractors are filtered out of visual WM. If distractors are filtered out they should not influence the amplitudes of these slow potentials. We can consequently infer from contralateral posterior slow potential pattern, whether filtering was successful. The increase in frontal activity should precede the effect of selection processes on contralateral slow potentials. In other words it should precede the time point where filtering is observable in the contralateral slow potentials. Such a frontal activity boost might then reflect a gatekeeper mechanism that controls access into visual WM. Furthermore, based on McNab and Klingberg’s (2008) findings, we hypothesize that the strength of the frontal activity will significantly predict visual WM capacity. Attentional control might determine how much relevant information a person can store. This relationship should be reflected in a correlation between the amplitude difference of frontal activity for distractor-present as compared to pure-target trials and measures of visual WM capacity.

In contrast to the design of McNab and Klingberg (2008), filtering in our task is not cued and hence preparation of filtering as reflected by the frontal boost should not start before the onset of the memory array. In order to differentiate between targets and distractors and hence decide if the present trial constitutes a distractor-present trial, all items have to be processed to a certain degree. During this initial perceptual processing, object-files for all items might be created and this might be observable in the electrophysiological components. In Experiment 1, a posterior positivity at about 200 ms after memory array onset was observed over contralateral as well as ipsilateral recording sites (see Chapters 5.3.2 and 5.4). Its amplitude increased as a function of the number of items until it reached an asymptote for four items. We reasoned that the amplitude of the posterior positivity reflects the number of created object-files. The observed asymptote is consistent with the assumption that humans can hold maximally four object-files at once (cf., Cowan, 2001; Pylyshyn, 2001; Scholl, 2009). This leads to the question about the fate of distractors in the current task. We assume that all items have to be processed to a certain degree to discriminate between targets and distractors. A look on Figure 3 of Vogel et al. (2005) indicates that distractors initially are processed in this type of task. Further evidence for this hypothesis would be a posterior positivity that is sensitive for the total number of items, irrespective if targets or distractors. Alternatively, object-files might not be created for distractors and hence the amplitude of the posterior positivity might depend on the number of targets only.

13.1 Results

Please recall that we ran the following conditions in the change detection task: 2T, 3T, 4T, 5T, 2T2D, 2T3D, 3T2D. Our data allow for three comparisons to analyze filter effects in the mean response accuracies and contralateral posterior slow potentials: Comparison 1 (2T, 4T, 2T2D), Comparison 2 (2T, 5T, 2T3D) and Comparison 3 (3T, 5T, 3T2D). If distractors are not filtered out they should influence mean accuracies as well as the amplitudes of slow potentials. In that case mean accuracies as well as slow potential amplitudes for distractor-present conditions and respective high-load conditions should not differ. If, however, distractors are filtered out to a certain degree, mean accuracies and slow potential amplitudes for distractor-present trials should lie in between the respective low-load and high-load conditions.

Three 3 (number of items) ANOVAs on mean response accuracies for the three comparisons yielded a significant effect of the number of items, all Fs > 96.41 all $p_{corr} < .001$. For all three comparisons, mean accuracies were highest for respective low load conditions, significantly worse for distractor-present conditions and worst for respective high load conditions (2T > 2T2D > 4T; 2T > 2T3D > 5T; 3T > 3T2D > 5T; means: 2T = .97; 3T = .91; 4T = .85; 5T = .78 ; 2T2D = .94; 2T3D = .90; 3T2D = .86), all Fs > 16.83, all ps < .001, indicating that distractors were filtered out to a certain degree.

Figure 13.1B reveals a pronounced posterior positivity at PO3/4 in the time window from about 200-260 ms, whose amplitude is a function of the number of items—regardless if targets or distractors—but reaches an asymptote for four items. A 2 (hemisphere) × 7 (number of items)-ANOVA on the posterior P2 in the time window from 200-260 ms at electrode PO3/4 yielded a significant main effect of hemisphere, $F(1,39) = 7.32$, $p < .05$, $\eta^2_{partial} = .16$ and a significant main effect of the number of items, $F(6,234) = 42.98$, $\varepsilon = .70$, $p_{corr} < .001$, $\eta^2_{partial} = .52$. These factors did not interact, $F(6,234) = 1.47$, $\varepsilon = .82$, $p_{corr} = .20$, $\eta^2_{partial} = .04$. For contralateral as well as ipsilateral recording sites, set sizes 2T, 3T and 4T differed from each other, all Fs > 36.76, all ps < .001 and all Fs > 37.14, all ps < .001, respectively, but 4T did not differ from 5T, $F(1,39) = 0.00$, $p = .95$ and $F(1,39) = 0.02$, $p = .89$, respectively. For both hemispheres, there is a linear trend from 2T to 4T,

$F(1,39) = 107.06$, $p < .001$ and $F(1,39) = 126.20$, $p < .001$, respectively, without quadratic part, $F(1,39) = 0.00$, $p = .99$ and $F(1,39) = 1.57$, $p = .22$, respectively. This indicates a constant increase in amplitude from 2t to 4T, where the asymptote is reached. Furthermore, for both hemispheres, the distractor-present trials did not differ in amplitude from the respective pure-target trials (2T2D=4T; 2T3D=3T2D=5T), all *F*s < .64, all *p*s > .43 and all *F*s < 1.33, all *p*s > .26, respectively, indicating that all items were processed to the same degree, regardless if target or distractor (see Figure 13.2).

As expected, there was a frontal negativity starting at about 230 ms after onset of the memory array, that differentiated between distractor-present and pure-target trials (see Figure 13.1A). The effect was clearest at electrode F7/8. We conducted a 2 (hemisphere) × 7 (number of items)-ANOVA on the amplitude of the frontal negativity within the time window from 230-300 ms at electrode F7/8 (see Figure 13.3). There was a significant effect of hemisphere, $F(1,39) = 16.06$, $p < .001$, $\eta^2_{partial} = .29$. Ipsilateral activity was overall more positive as compared to the contralateral one. Additionally there was a significant effect of the number of items, $F(6,234) = 50.14$, $\varepsilon = .80$, $p_{corr} < .001$, $\eta^2_{partial} = .56$. These factors did not interact, $F(6,234) = 0.85$, $\varepsilon = .80$, $p_{corr} = .51$, $\eta^2_{partial} = .02$. The effect of the number of items goes back to a significant difference between pure-target trials (2T, 3T, 4T, 5T) and distractor-present trials (2T2D, 2T3D, 3T2D) for the contralateral as well as ipsilateral frontal negativity, $F(1,39) = 129.44$, $p < .001$ and $F(1,39) = 188.83$, $p < .001$, respectively. The amplitudes at contralateral as well as ipsilateral frontal recording sites did clearly not differ between distractor-present trials, for five out of six contrasts, all *F*s < 1.22, all *p*s > .27; the remaining contrast (2T3D vs. 3T2D over ipsilateral recording sites) was marginally significant, $F = 3.36$, $p = .07$. With one exception, amplitudes in the pure-target trials do not differ from each other either: Amplitudes for set size two are more positive as compared to the other pure-target trials (3T, 4T, 5T) for contralateral as well as ipsilateral recording sites, $F(1,39) = 6.77$, $p < .05$ and $F(1,39) = 4.80$, $p < .05$, respectively. All other pure target-trials elicit an equal amplitude for contralateral as well as ipsilateral recording sites, all *F*s < 0.45, all *p*s > .50. There is a higher positivity for set size 2 as compared to the other pure-target trials, whereas amplitudes in distractor-present trials are more negative as compared to the pure-target trials. Therefore, it is rather improbable that the amplitude modulation for set size 2 is related to the filter mechanism and will not be further discussed in the following.

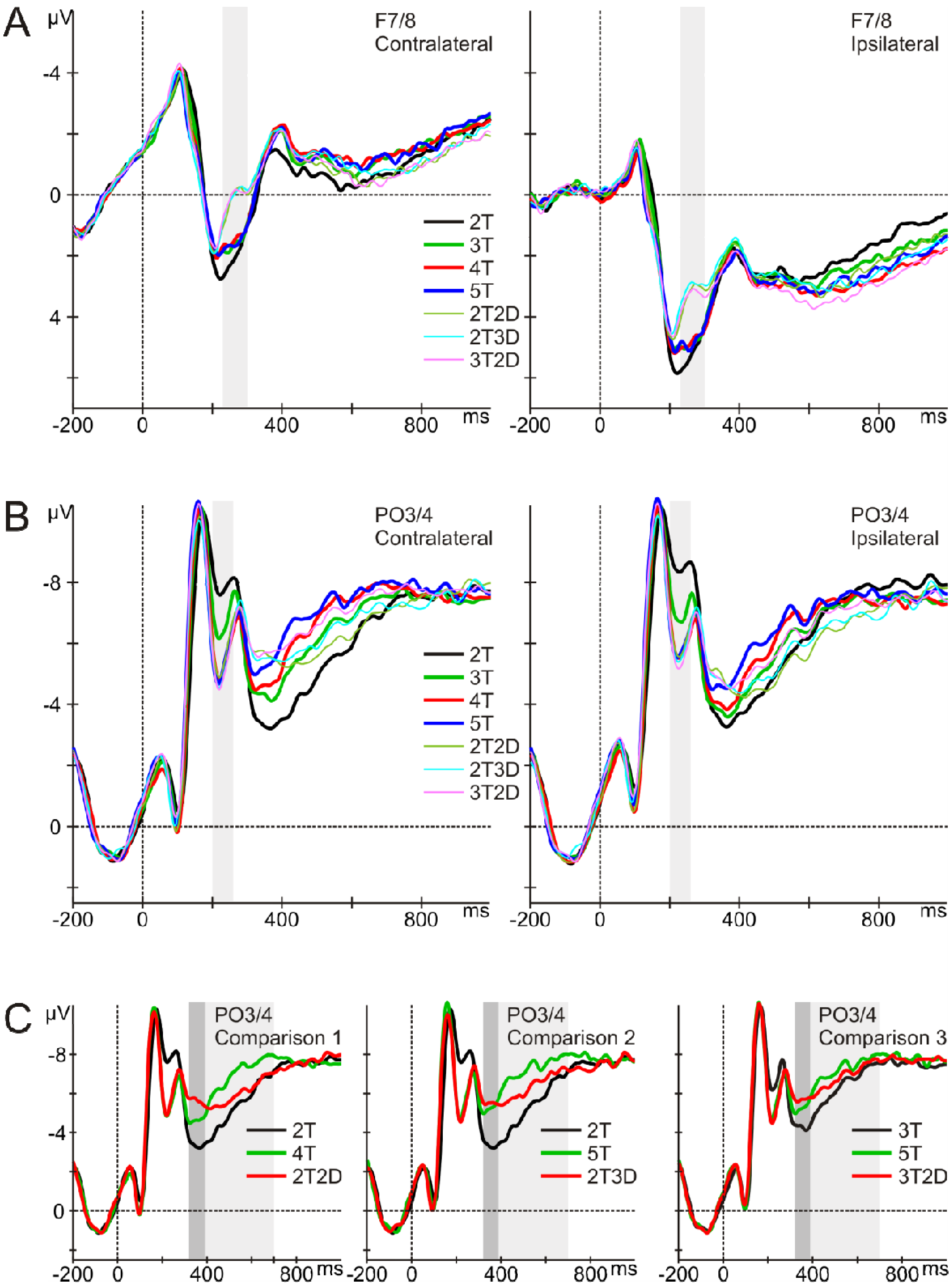

Figure 13.1. The time-course of filtering. (A) Grand averaged frontal negativity relative to the onset of the memory array at F7/8. (B) Grand averaged posterior positivity relative to the onset of the memory array at PO3/4. For (A) and (B), colors code the number of items. Thick lines code pure-target trials; thin lines code distractor-present trials. (C) Grand averaged contralateral slow potentials relative to the onset of the memory array at PO3/4. Colors code the numbers of items.

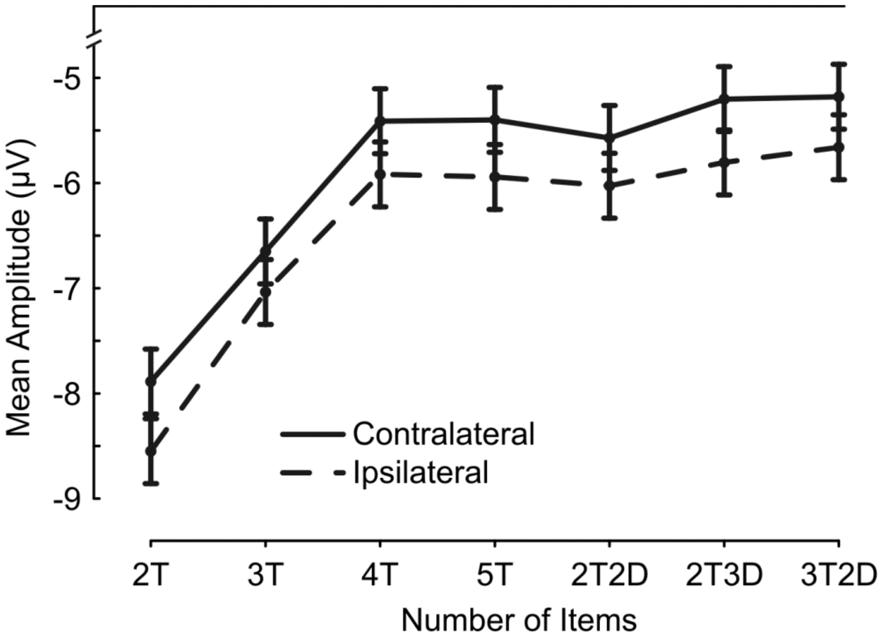

Figure 13.2. Posterior positivity as a function of hemisphere and the number of items. The displayed 95%-confidence intervals are based on the main effect of number of items.

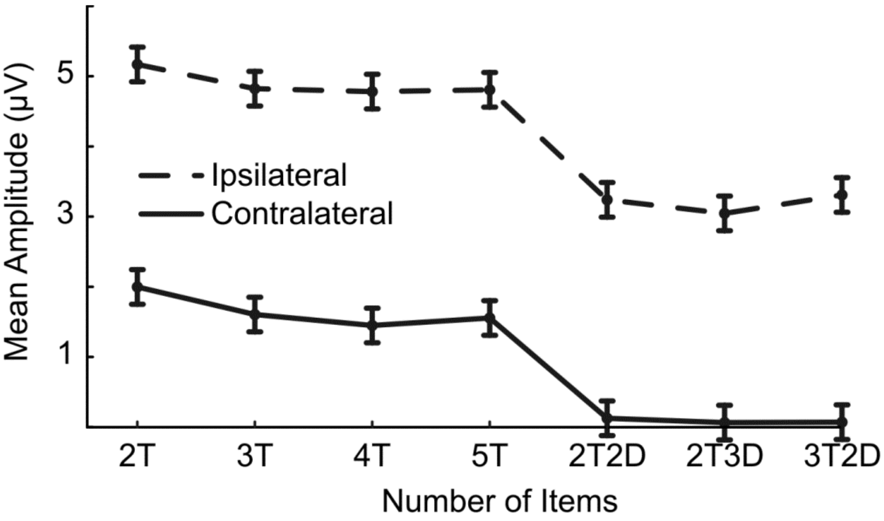

Figure 13.3. Frontal negativity as a function of hemisphere and the number of items. The displayed 95%-confidence intervals are based on the main effect of number of items.

To test the hypothesis that the strength of this frontal boost predicts WM performance, we calculated the difference in amplitude between pure-target and distractor-present trials for the contralateral as well as ipsilateral negativity for each participant. This amplitude difference in contralateral and ipsilateral negativity correlated significant with K_{max}, $r = .48$, $p < .01$ and $r = .41$, $p < .01$, respectively and with mean accuracies, $r = .41$, $p < .01$ and $r = .34$, $p < .05$, respectively.

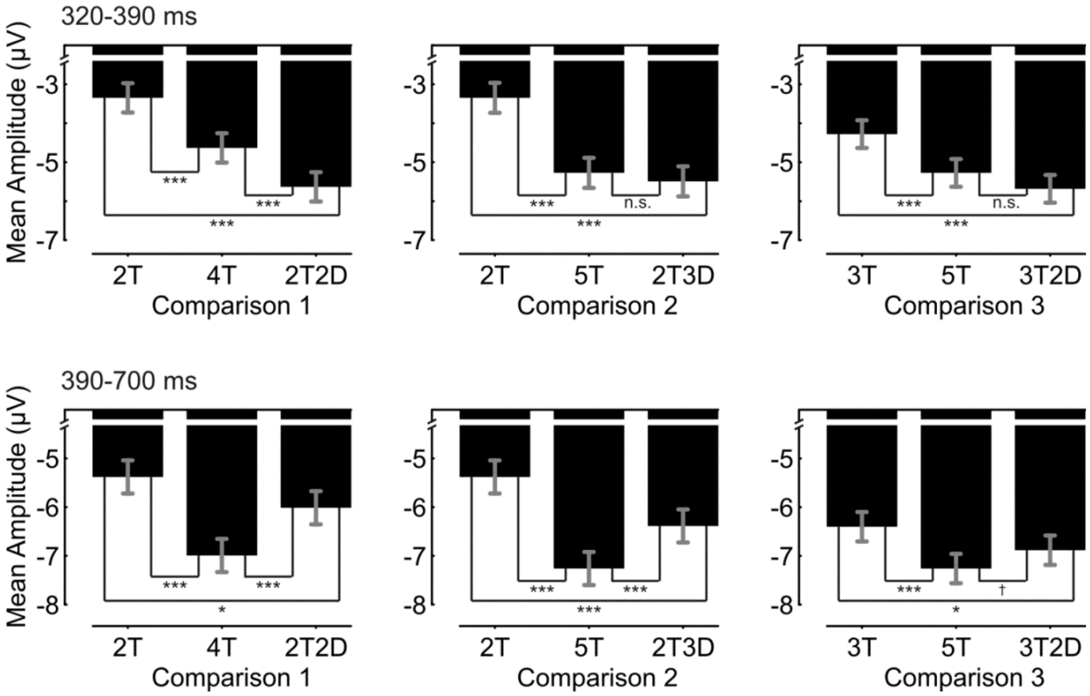

Figure 13.4. Contralateral slow potentials as a function of the number of items for each comparison in Time Bin 1 (320-390 ms) and Time Bin 2 (390-700 ms).

Figure 13.1C shows the contralateral slow potentials for the three comparisons (Comparison 1: 2T, 4T, 2T2D; Comparison 2: 2T, 5T, 2T3D; Comparison 3: 3T, 5T, 3T2D). In the training study, amplitudes are analyzed in the time window from 320-700 ms at electrode site PO3/4. A look on Figure 13.1.C reveals that contralateral slow potentials initially (between about 320-390 ms after onset of the memory array) do not differ between the distractor-present conditions and respective high-load conditions. From 390 ms on, amplitudes in the distractor present conditions approach those in the respective low load conditions, indicating the expected effect of filtering. Analyses of contralateral slow potential activity were therefore conducted on two time intervals, 320-390 ms and 390-700 ms after onset of the memory array. To analyze the amplitude modulations of contralateral slow potentials separately for the three comparisons, we conducted six ANOVAs on slow potential amplitudes at PO3/4, one for each of the three comparisons in each of the two time windows. Three 3 (number of items)-ANOVAs on contralateral slow potentials at PO3/4 in the first time window from 320-390 ms yielded a significant effect of the number of items for Comparison 1, $F(2,78) = 36.84$, $\varepsilon = .79$, $p_{\text{corr}} < .001$, $\eta^2_{\text{partial}} = .49$, Comparison 2, $F(2,78) = 37.16$, $\varepsilon = .86$, $p_{\text{corr}} < .001$, $\eta^2_{\text{partial}} = .49$, as well as Comparison 3, $F(2,78) = 16.33$, $\varepsilon = .89$, $p_{\text{corr}} < .001$, $\eta^2_{\text{partial}} = .30$. Furthermore, three 3 (number of items)-ANOVAs on contralateral slow potentials at PO3/4 in the later time window from 390-700 ms yielded a significant effect of the number of items for Comparison 1, $F(2,78) = 22.55$, $p < .001$, $\eta^2_{\text{partial}} = .37$, Comparison 2, $F(2,78) = 30.31$, $p < .001$, $\eta^2_{\text{partial}} = .44$, as well as Comparison 3, $F(2,78) = 8.03$, $p < .001$, $\eta^2_{\text{partial}} = .17$.

Please refer to Figure 13.4 for the respective contrasts. As can be seen in Figures 13.1C and 13.4, in the first time window slow potential amplitudes for the distractor-present conditions are equal or even higher than those for the respective high-load conditions for all three comparisons, indicating that the distractors are not yet filtered out. Contrary, in the later time window, the amplitude for the distractor-present conditions lies in between the respective low-load and high-load conditions, indicating that distractors are filtered out to a certain degree.

13.2 Discussion

Visual WM capacity is discussed to depend on a person’s ability to efficiently control attention. The better a person is able to control which items enter WM, the less items are unnecessarily consuming the highly limited capacity (cf., e.g., Awh & Vogel, 2008; Engle, et al., 1999; Vogel et al., 2005). Prefrontal structures might accomplish this gatekeeper function and act as a filter which controls entrance into WM (e.g., Awh & Vogel, 2008). Indeed, in a change detection task, McNab and Klingberg (2008) observed an increase in prefrontal activity preceding distractor-present trials but not pure-target trials. Furthermore, the strength of this activity was predictive for visual WM capacity. The authors interpreted this prefrontal activity as a mechanism that controls access to WM. Additionally, Vogel et al. (2005) discuss prefrontal activity as possible gatekeeper that controls which information enters visual WM in the lateralized change detection task with distractors. However, frontal participation in this task has not yet been tested. We investigated whether there exists frontal activity that might exert control over what information is given access into visual WM. We observed a frontal negativity—only in distractor-present and not in pure-target trials—that started about 230 ms after onset of the memory array and lasted about 70 ms. Hence, it preceded the posterior contralateral slow potentials. Furthermore, the strength of this component was predictive of visual WM capacity. The observed result pattern is perfectly in line with the assumption of a prefrontal mechanism that acts as a gatekeeper into visual WM and hence determines what information will be stored in visual WM. The measured frontal activity might constitute the neuronal implementation of this selection mechanism. In that way, attentional control might determine how much relevant information a person can store.

Although we used a lateralized design, the frontal biasing signal was equally pronounced over contralateral as well as ipsilateral recording sites. However, even though the initial processing of the items is lateralized due to the construction of the visual system, a topographic organization in frontal areas is rather improbable. Furthermore, the frontal activity seems not to reflect stimulus processing per se, but instead is more in line with an executive control signal.

Posterior contralateral slow potentials, starting about 300 ms after memory array onset initially reflect the processing of all items, independent if target or distractor. In line with the claim that the frontal activity acts as a gatekeeper to prevent unnecessary storage, the filtering out of distractors is evident in the posterior slow potentials at about 390 ms, that is 90 ms after the offset of the frontal activity boost.

Slightly before the onset of the frontal biasing signal, at about 200 ms after memory array onset, a positive component emerged at posterior electrode sites. Its amplitude varied, in line with the results of Experiment 1, as a function of the number of items and reached its asymptote for four items. Interestingly, it did not differentiate between targets and distractors. This indicates that at this point in time all items are processed to a certain degree.

To conclude, exploiting the high temporal resolution of the EEG, we were able to track the time course of filtering in the change detection task with distractors. Initially, all items are processed to a certain degree as reflected in the posterior positivity around 200 ms after memory array onset. The ensuing frontal activity initializes the filtering out of distractors to prevent their storage in visual WM. About 90 ms after this frontal signal, filtering out of distractors is observable in posterior contralateral slow potentials, supporting our claim that the frontal activity might send a biasing signal to prevent storage of unnecessary information in visual WM.

Part 5

General Discussion

14 Overview

Two main topics constitute the focus of the present work. Firstly, we attempted to carefully characterize and compare posterior slow potentials and the CDA for a deeper understanding of their functional significance. We will discuss the impact of posterior slow potentials, namely, their fit with behavioral data as observed in our experiments, but also their potential contamination through task-general processes such as effort. A comparison of the slow potentials and the CDA will illustrate the respective advantages and disadvantages of both components as measures of visual WM processes. One further issue of the current work was the function of ipsilateral delay activity. Here, we will work out how this question might be further addressed. Additionally, we will discuss the different contribution of load-dependent ipsilateral delay activity over experiments. Discrepancies between experiments might account for the presence or absence of ipsilateral delay activity. A third chapter will deal with the transient nature of load-effects in the slow potentials as well as the CDA in our data and corresponding observations in the literature.

A second main issue in the current work was the operation of selection mechanisms in the service of effective visual WM. These mechanisms constitute a highly important factor for visual WM functioning. Experiment 3 addressed the investigation of the plasticity of selection mechanisms in visual WM. Although we did not observe specific training-induced changes after a two-week MOT training, we observed overall improvements in filter ability from pre to post training session. This constitutes evidence that selection mechanisms in visual WM are indeed plastic. Based on the results of the training study, we can exclude that sustained attention towards targets and the prevention of attentional capture through distractors is the crucial selection process in the change detection design we employed. Here, we will categorize the in the literature employed types of selection criteria for filtering distractors in the change detection task. We conclude that the specific type of selection criterion exerts influence on the underlying attentional processes. Based on these considerations, we discuss an alternative hypothesis about the selection mechanism in the change detection design which we employed. Furthermore, we will discuss that the memory array of the change detection task with distractors as employed in Experiment 3 actually constitutes a visual search display. We will outline how to benefit from existing research on the visual search paradigm in the investigation of filtering in visual WM.

Last but not least, the interplay of visual WM with attention will be discussed. Attentional processes were repeatedly of interest in the current work. In particular, attention plays a role as gatekeeper during initial entrance into visual WM as well as a rehearsal mechanism in form of sustained attention during maintenance. In this context, we will also recapitulate the role of the CDA as an attentional pointer during visual WM maintenance.

15 The Importance of Slow Potentials for the Investigation of Visual Working Memory

The working unit of Vogel (e.g., Vogel & Machizawa, 2004; McCollough et al., 2007) attempts to examine visual WM processes with the aid of the CDA. This is a valuable approach as the CDA has crystallized out to be a particularly promising component in the investigation of visual WM maintenance. The attractive logic of the contralateral control method is that the CDA can be extracted as a component that is—contrary to the posterior slow potentials—pure with respect to the process of interest, the maintenance of visual information in WM. This apparent characteristic makes it a well suited working ground for the further investigation of visual WM functioning. However, an alternative approach might be the further and deeper investigation of the role of posterior slow potentials for visual WM functioning. Although the slow potentials have the major disadvantage that they potentially are contaminated through other non-mnemonic processes, they also offer several not-to-be-neglected benefits. Here, based on the results of the conducted experiments advantages as well as disadvantages of the slow potentials will be discussed. We plead in favor of using slow potentials as independent components in the research of visual WM functioning and not just as the building blocks of the CDA.

15.1 The Influence of Task-General Processes

In line with the claim that contralateral slow potentials mirror the maintenance of information held in visual WM, their amplitudes have been shown to be a function of the amount of relevant items. However, task difficulty, arousal and the amount of effort might also increase with the number of relevant items and might therefore be confounded with memory load. Consequently, the amplitude modulation of slow potentials can in principle also be explained by these factors (cf. Chapter 3).

Participants in Experiment 2 encountered more difficulties as memory load increased, as indicated by an increased error rate. This increased difficulty might increase the amount of general arousal and effort. Fortunately, Vogel and colleagues (e.g., Vogel & Machizawa, 2004) have shown that task difficulty, arousal and effort do not cause lateralized activity. Therefore, the absent effect of the number of relevant items on ipsilateral slow potentials in the data of Experiment 2 gains further importance. If task difficulty, arousal and effort influence slow potential activity bilaterally and there is no ipsilateral slow potential activity due to the relevant items (in Experiment 2), it would appear that these factors do not influence posterior slow potentials at all.

The data of Experiment 2—seen individually—are consistent with the claim that slow potentials are not contaminated by these task-general effects. However, contrary to Experiment 2, in Experiments 1 and 3 we observed load-dependent ipsilateral slow potential activity (for a discussion of these observed differences in contribution of ipsilateral delay activity, see Chapter 16.1). Therefore, the for Experiment 2 made conclusion concerning a contribution of task-general processes to slow potential activity does not apply to the latter two experiments. The observation of bilateral load-effects that does not reach an asymptote with visual WM capacity does not allow excluding a contamination of observed slow potential activity through task-general effects, such as effort. However, as already discussed in Experiment 1, these effort-effects are actually quite interesting. Although, in Experiment 1, we were not able to disentangle effects of higher effort from effects of improvements in maintenance in the slow potential activity under incentives, we were able to conclude that the improved visual WM capacity under incentives was reflected in these slow potentials. In particular, slow potentials were more negative under incentives as compared to the baseline condition, an effect described as cognitive effort (Rösler et al., 1997). Maybe, the two aspects, the amount of invested effort and the resulting increase in maintenance cannot be dissociated at all. The process of visual WM maintenance which is reflected by the slow potentials might mirror the amount of invested effort as well as the resulting amount of maintained information. In that case, effort would not constitute a task-general process that can be subtracted out, but rather would be a part of the maintenance process per se. The amount of cognitive effort (Rösler et al., 1997) might be inextricably interwoven with the amount of maintained information. Calculating a CDA might therefore lead to a subtraction of a part of the maintenance process. The contralateral control method might throw out (part of) the baby with the bath water.

We observed one example of such a problematic consequence of the CDA extraction in our data. A look on Figure 11.3 reveals that contralateral and ipsilateral slow potential activity is equal for set size 2 in Experiment 1 as well as Experiment 3. Consequently, the resulting CDA amplitude is zero. This constitutes a critical consequence for the interpretation of the

CDA. If, according to Vogel and colleagues (e.g., Ikkai et al., 2010; McCollough et al., 2007; Vogel & Machizawa, 2004) the amplitude of the CDA mirrors the amount of represented items in visual WM, it should constitute a ratio-scaled measure and therefore the zero point should be interpretable. Consequently, our result would imply that no items are maintained in visual WM in case of set size two. Obviously, this is implausible; participants indeed maintained these two items in visual WM. We assume that this maintenance was reflected in the slow potentials, but rejected by the calculation of the CDA.

15.2 The Slow Potentials' Relation to Response Accuracies

In Experiment 1 we observed an increase in behaviorally measured visual WM capacity under incentives as compared to the baseline condition. Obviously, participants enhanced their performance under reward anticipation. Interestingly, this increase in visual WM capacity was reflected in the posterior slow potentials only and not in the CDA. Slow potential amplitudes, in contrast to CDA amplitudes, significantly increased under incentives indicating an improved visual WM functioning. This coherency between behavioral capacity increases and corresponding increases in slow potential amplitudes was further demonstrated in a correlation between the amount of increase in slow potential activity from three to four items and the behaviorally measured visual WM capacity in the incentive condition. Furthermore, in Experiment 3 there was a behavioral training effect in form of a specific behavioral improvement in the filter condition. In the post training session, participants were better able to ignore the distractors. Here again, the behavioral improvement was mirrored by slow potential activity, but not by CDA activity. In the post training session, slow potential amplitude decreased exclusively in the filter condition, indicating—just like the behavioral data pattern—the improved filter ability.

To conclude, posterior slow potentials—additionally to the CDA—are worth considering in the investigation of visual WM functioning. In line with our data, they are discussed to reflect cognitive effort (Rösler et al., 1997). Obviously, they mirror, possibly among other things, an important process, essential for visual WM functioning and leading to good performance in visual WM tasks that is not reflected in the CDA, at least in our data. However, the drawback remains, that we hardly know anything about the nature of this process. A profound investigation of the nature of this process would deliver a more holistic picture of the processes running during visual WM maintenance.

A further advantage of the slow potentials as a measure of visual WM functioning is that they can be extracted in a standard change detection task. It constitutes a multitude of additional degrees of freedom when memory processes do not only have to be investigated lateralized. For example, the presentation time of the memory array can be prolonged, which opens the possibility to present more complex objects with more features that have to be encoded. Additionally, the array can be enlarged because there are no longer constraints of parafoveal vision.

16 Ipsilateral Delay Activity

The CDA is currently considered as one of the most promising electrophysiological components in visual WM research. However, if we want to use this component to get to know more about memory processes, its interpretation should be validated. Set size dependent ipsilateral delay activity that we observed in all of our experiments, however, constitutes a problem for the interpretation of the CDA. One of the key questions of this dissertation project was what this ipsilateral delay activity actually reflects. Knowing about the origin of set size dependent ipsilateral slow potential activity would help interpreting the CDA. We already discussed this question in the context of the results of Experiment 1 and 2. Now, we want to take it up again and further illuminate it.

16.1 Comparing Ipsilateral Delay Activity Patterns across Experiments

We observed ipsilateral delay activity in each single experiment. In Experiment 1 and 3, ipsilateral slow potentials were a function of the number of to-be-remembered items. Interestingly, in Experiment 2, we observed a modulation of ipsilateral delay activity only in a special case. Only when participants remembered one single relevant item, ipsilateral slow potentials' amplitudes were modulated as a function of the number of presented irrelevant items. When participants had to remember more than one relevant item, ipsilateral slow potentials' amplitudes were neither influenced by the number of relevant nor by the number of irrelevant items. In all of these latter conditions, it was of equal amplitude. What might be the difference between Experiment 2 and the other two experiments, leading to these differences in ipsilateral contribution?

The pure-target conditions in the change detection task of Experiment 3 (set sizes 2, 3, 4, or 5) constitute a good replication of Experiment 1 (set sizes 2, 3, 4, 5, or 6). As load-dependent ipsilateral slow potential amplitudes emerged in both experiments (see Chapters 5.3.2 and 11.1), it seems rather probable, that differences in design between these two experiments and Experiment 2 account for the observed differences in ipsilateral delay activity.

Maybe, the imbalanced design of Experiment 2 makes it easier to inhibit the irrelevant hemifield. As already discussed in Experiment 2, when only one relevant item has to be remembered, this inhibition mechanism is not necessary, leading to the observed processing of irrelevant items in trials with relevant set size one. However, when two or three relevant items are processed, the imbalanced design might help focus attention towards the relevant hemifield. A further difference between Experiment 2 on the one hand and Experiments 1 and 3 on the other hand might be their overall difficulty. In the latter two experiments, we ran conditions from two up to six, or five to-be-remembered items, respectively. Contrary, in Experiment 2, we ran only conditions between one and three items, an amount of information well below most participants’ visual WM capacity. A task that easy as in Experiment 2 might have rendered an ipsilateral contribution to maintenance unnecessary.

A first step to decide between the two just outlined possible reasons for the observed differences in ipsilateral delay activity between experiments might be to investigate the same imbalanced design as in Experiment 2, but with higher set sizes. For example, one might employ a 3 (relevant items) × 3 (irrelevant items) design with three, four and five items. If, on the one hand, the first assumption is right, namely that the imbalanced display helps in allocating attention towards the relevant hemifield, we would anticipate the same result pattern as in Experiment 2, namely that irrelevant items are filtered out. On the other hand, if ipsilateral delay activity reflects the additional engagement of the ipsilateral hemisphere when the task becomes more demanding, having a more demanding design should reveal ipsilateral load-dependent slow potentials also in an imbalanced display.

A third interpretation—although highly speculative—for the observed differences between experiments, is that participants in Experiment 2 maybe, additionally to using their visual WM for colors, recoded the colors into verbal or conceptual chunks. Some participants reported after the experiment, that they used the strategy to remember “banners” for set size 3. They remembered for example “France”, that means, “red, blue, white”. This strategy might have helped to be better able to filter out the items on the irrelevant display side. Recoding and chunking a small number of colors seems to be feasible. However, this strategy might not have been applied in Experiments 1 and 3, because it might not be efficient for a larger number of items. Firstly, 100 ms presentation time might not be enough time for chunking a larger number of items. Secondly, the colors of banners for different countries are part of participants’ general knowledge and therefore constitute long-term memory entries as a basis for chunking of three items. Contrary, no equivalent long-term memory entries usually exist that might form a basis for chunking of four or more colors.

Further testing is necessary to unravel the reason for the different patterns of ipsilateral delay activity over experiments. Anyway, ipsilateral delay activity in Experiment 2 seems to deviate from the usual pattern. Therefore, in the next chapter we concentrate on the results of Experiment 1 and 3, where we employed the commonly used design with an equal number of items in both hemifields.

16.2 Processing of Relevant or Irrelevant Items?

In Chapter 12.1, we conducted an analysis restricted to the pure-target trials of the lateralized change detection task (set sizes 2, 3, 4, and 5) employed in Experiment 3. This experiment constitutes a good replication of Experiment 1 (lateralized change detection task with set sizes 2, 3, 4, 5, and 6). In both experiments, the amplitude of ipsilateral delay activity varied as a function of the number of presented items. Additionally, increases in ipsilateral slow potential amplitudes with increasing set size were less pronounced as compared to corresponding increases in contralateral slow potential amplitudes in both experiments (see Figure 11.3). The exact replication of the data pattern from Experiment 1 constitutes evidence for the existence of load-dependent ipsilateral delay activity in the standard version of the lateralized change detection task with balanced visual input in both hemifields. However, the critical question is what does this ipsilateral activity reflect? Recall that we already aimed to solve this question in Experiment 2. However, as outlined in the preceding chapter, results of Experiments 1 and 3 indicate that the specific design of Experiment 2 might have somehow influenced the result pattern. Therefore, we reevaluate the question about the function of ipsilateral delay activity and develop experimental designs for its further investigation.

As already outlined in Experiment 2, load-dependent ipsilateral delay activity might either reflect the processing of relevant items or the processing of the irrelevant items. Even a third hypothesis is possible; it might only reflect an increase of task-general processes (such as effort) with increasing set size. Actually, in light of our data that speak in favor of the two other hypotheses, we do no longer believe in this possibility. Please recall that when only one relevant item had to be processed in Experiment 2, irrelevant items were not filtered out but processed to a certain degree and caused the load-effects on the ipsilateral delay activity. Furthermore, the incentive effects in contralateral as well as ipsilateral slow potentials in Experiment 1 where—based on the fit with behavioral data—interpreted with enhanced maintenance. To conclude, it seems quite safe for us to assume that ipsilateral delay activity is—at least in parts—memory-specific. The further investigation of the nature of ipsilateral delay activity will contribute to a better understanding of the processes running during the retention interval of the lateralized change detection task. Furthermore, their nature has highly important implications concerning the nature of the CDA as already detailed in the introduction to Experiment 2 (Chapter 6.1). When contralateral as well as ipsilateral delay activity reflect—at least in part—maintenance processes, these processes are partially subtracted out in the CDA.

In Experiment 2, we already collected empirical evidence from the literature for both hypotheses, that ipsilateral delay activity might reflect the processing of relevant vs. the processing of irrelevant items. However, in light of recently published studies we here make a further attempt to explain in how far the processing of the irrelevant items might cause the ipsilateral delay activity.

Imagine you are performing the lateralized change detection task. At the time point of the items' appearance, you have a perceptual sensation of several items in the right and the left hemifield. Independent of the WM-task at hand, you would always be able to report afterwards, that items have been present in the irrelevant hemifield. In other words, if there were some trials, without any items in the ipsilateral hemifield, you also could easily report their absence. To conclude, the irrelevant items are processed to a certain degree. Probably, you might not be able to retrieve any specific details about the irrelevant items, but you can decide that "they have been there". Furthermore, maybe you might even retain an impression of the spatial arrangement of the irrelevant items on the display. And this might exactly be what ipsilateral delay activity reflects: the individuation and consolidation of core object-files in the irrelevant hemifield. In line with this reasoning, Xu and Chun (2006, 2009) differentiate between two processes during visual WM maintenance: An individuation process with a neuronal basis in the inferior IPS and an identification process with a neuronal basis in the superior IPS. During the individuation, up to four core prototypes of objects are separated based on their location. The features of these objects are then further processed during the identification process and full-fledged detailed object representations arise (Xu & Chun, 2009). Importantly, the authors observed sustained activity in both, inferior as well as superior IPS dependent on the number of to-be-remembered items (Xu & Chun, 2006). The sustained nature of the activity of inferior IPS implicates that the individuation process is not a transient process which ends after a while and is followed by the identification process. Instead, both processes seem to run in parallel. The ipsilateral load-dependent delay activity as observed in our data might mirror exactly this sustained individuation process of the items in the irrelevant hemifield. The processing of the relevant items might elicit more pronounced activity, mirrored by the contralateral slow potentials, because additionally to the individuation process, these items are further processed to gain full-fledged object representations.

Data of a recent combined EEG and MEG study (Mitchell & Cusack, 2011) speak in favor of this hypothesis. The authors employed a lateralized change detection task for colors. With the aid of both methods, additionally to lateralized components, also bilateral components were observed whose amplitude increased with increasing set size up to WM capacity limits (see also Robitaille et al., 2009). The authors assume that the activity observed over contralateral as well as ipsilateral recording sites might mirror an early individuation process, while the additional contralateral activity might have a closer link to WM maintenance processes. Furthermore, the bilateral activity as a function of set size is strongest during the early retention interval and at that time the posterior IPS was identified as the underlying source. The authors argue that this is a further indication, that the bilateral activity might stand for the individuation of the objects and the more sustained contralateral activity might reflect visual WM maintenance processes.

We just outlined that ipsilateral delay activity might mirror the processing of items in the irrelevant hemifield. But, there is the caveat that working memory capacity is known to be restricted to about four items (e.g., Cowan, 2001; Luck & Vogel, 1997). An implication of our hypothesis, however, is that participants would store—at least some information—about several objects in the left and the right hemifield and thereby this limitation would often be exceeded. If, for example, three items are presented in each hemifield in the lateralized change detection task, participant would have to be able to store at least information about six rough object-files in visual WM. Interestingly, there are indeed hints, that the human brain has independent resources for the maintenance of information in the left and right hemifield. Performance is better when information is divided into both hemifields as compared to a unilateral presentation (Delvenne, 2005; Umemoto et al., 2010). This speaks in favor of the existence of independent resources for each hemisphere that contribute to the maintenance process. In that way, there might be a resource for the processing of the items in the relevant hemifield of the lateralized change detection task reflected by the contralateral slow potentials and another, independent resource for the processing of the items in the irrelevant hemifield reflected by the ipsilateral slow potentials. There are further observations that are highly interesting in the light of the current hypothesis: Alvarez and Cavanagh (2005) observed that participants are able to track twice as many targets in a MOT task in a condition where the targets are divided into the left and the right hemifield as compared to a condition where all targets are shown within one hemifield. Based on the observation of Alvarez and Cavanagh (2005), Delvenne (2005) investigated whether WM capacity can also be enhanced when presenting the memoranda within two hemifields. Using a change detection design he examined WM for colors and locations. He observed only an increase in WM capacity for the location-task and not for the object-task and concluded that the selection of stimuli based on their location, which is crucial in MOT as well as a spatial change detection task, is mediated by independent resources for the two hemifields. Recently, he replicated the data pattern for the maintenance of color information in a lateralized version of the change detection task. Visual WM for colors was not better when the memoranda were presented within two hemifields (Delvenne, 2011), indicating that detailed feature information is processed by one resource shared between hemispheres. Taken together, the data indicate that resources that exist independently for each hemisphere might process spatial information whereas shared resources might process object information. Transferred to our hypothesis, location information of core object-files (the individuation) might be reflected by the contralateral slow potentials for the relevant items and by the ipsilateral slow potentials for the irrelevant items. Additional and more precise object-identification takes only place for the relevant items and leads to the additional activity for contralateral slow potentials.

Mitchell and Cusack (2011) observed lateralized as well as bilateral activity in the lateralized change detection task. The same was observed by Robitaille et al. (2009, 2010). Actually the data of all three studies allow for both hypotheses, a contribution of the relevant as well as the irrelevant items to ipsilateral delay activity, because in all studies the number of relevant and irrelevant items is always the same. Additional testing is necessary to decide between both hypotheses. Actually, the design of Experiment 2—deconfounding the number of items in the relevant and irrelevant hemifield—was a step in the right direction. However, the design raised problems and affected the contribution of ipsilateral delay activity, already discussed in the preceding chapter. But how could we further approach an answer?

Interestingly, Xu (2008) designed an fMRI experiment that—redesigned as an EEG experiment—might actually be a perfect test of the hypothesis that ipsilateral delay activity reflects the processing of the irrelevant items. They presented their participants three conditions of memory arrays in a standard change detection task for objects: (a) one item, (b) four items with different shapes at different locations and (c) four times the same item at four different locations. During test, one object was presented and participants' task was to indicate whether it was old or new. Interestingly they observed—in line with their theory of object individuation and identification as outlined above—different patterns in the inferior and superior IPS. Activity in the inferior IPS was higher whenever four items were on the screen as compared to one item, independent of the items' identity. Contrary, activity in the superior IPS was higher for the condition with four different items as compared to the other two conditions. Here, the condition with four times the same item resulted in a similar activation strength as the condition with only one item. This design can be employed for the test of the hypothesis that ipsilateral delay activity reflects the individuation of items in the irrelevant hemifield of the lateralized change detection task. The design would include the following conditions: (a) one item in each hemifield, (b) four items with different shapes in each hemifield, and (c) four times the same item in each hemifield. With this design the number of to-be-individuated and the number of to-be-identified objects are varied independently. Measured slow potential activity should result in the following pattern: The standard pattern for (a) and (b), that means contralateral as well as ipsilateral slow potentials are more negative when four items are presented as compared to one item and this pattern is less pronounced for ipsilateral slow potentials as compared to contralateral ones. Condition (c) constitutes the critical test: ipsilateral slow potential activity should not differ between conditions (b) and (c), because both times, four objects have to be individuated. Contrary, contralateral slow potential activity should differ for (b) and (c). Here too, during individuation in both conditions four items are localized. But, crucially, contralateral slow potentials should additionally reflect the process of object identification for the relevant items. In condition (c) only one shape has to be identified whereas four shapes have to be identified in condition (b). Therefore, contralateral slow potentials should be smaller in condition (c) as compared to (b). The observation of this data pattern would clearly prove that ipsilateral delay activity is caused by the processing of irrelevant items. It further would show that these items are individuated as core object files based on their location, without further detailed feature processing.

17 Delay Activity—Transient or Sustained?

Figures 5.3, 6.2, 6.4, 9.4 and 11.1 all indicate that load-effects on slow potential amplitudes in our experiments are of limited duration. At about 700 ms after the onset of the memory array, amplitudes for the various set sizes converge. Logically, the load-effects in the CDA that go back to load-effects on the contralateral slow potentials can also only last until about 700 ms (see Figures 5.2, 6.6 and 9.3; the late load-effects on the CDA in Experiment 2, Figure 6.6, are due to load-effects on ipsilateral slow potentials as already discussed in Chapter 6.4). Obviously, this pattern is actually not in conformity with the idea of delay activity in the service of WM. As delay activity is interpreted as the process that keeps information that is no longer in view active in WM, it should persist over the whole retention period.

Having a look on the literature, there are differences in the duration of the CDA amplitude as a function of memory load between experiments. The lab of Vogel (e.g., Jost, Bryck, Vogel & Mayr, 2011; McCollough et al., 2007; Vogel & Machizawa, 2004) constantly reports sustained CDA amplitudes as a function of load, starting about 300 ms after onset of the memory array and persisting until the end of the retention interval. They even report that the CDA lasts longer if the retention interval is prolonged, leading to CDA waves of up to 4.5 s (unpublished data as reported in Perez & Vogel, 2011). One exception where the working group of Vogel does not observe a load-dependent CDA until the end of the retention interval is the study of Ikkai et al (2010). In that study, CDA amplitudes converge for different set sizes about 150 ms prior to the ending of the retention interval (see Figure 3A of their study). All other research groups always observe load effects on CDA amplitudes that do not last until the end of the retention interval. For example, a look on Figure 2C in

Robitaille et al. (2010) reveals that the CDA amplitudes for different set sizes already converge at about 900 ms after onset of memory array (lateralized change detection task, 200 ms memory array, 1000 ms retention interval). Another study of these authors with similar task parameters shows a comparable pattern for posterior slow potentials (Robitaille et al., 2009, Figure 2A). In this study, the pattern is observable in the slow potentials and not in the CDA, because the CDA was not consistently extractable. Slow potential amplitudes for different set sizes for left as well as right electrodes converge already at about 900 ms after onset of the memory array (lateralized change detection task, 200 ms memory array, 1200 ms retention interval).

Table 17.1

Approximate Duration of Set Size-Effects on CDA Amplitude Relative to Memory Array Onset Estimated from Grand Averages (CDA), Duration of the Memory Array (Memory), Duration of the Retention Interval (Retention) and Gap between End of the Set Size Effect on CDA and End of Retention Interval (Gap) for the 3 Experiments of the Present Work and Additional Studies From the Literature.

Study	Memory	Retention	CDA	Gap
Experiment 1	100 ms	900 ms	350-700 ms	300 ms
Experiment 2	100 ms	900 ms	350-700 ms	300 ms
Experiment 3	100 ms	900 ms	320-700 ms	300 ms
Robitaille et al., 2009	200 ms	1200 ms	500-900 ms (slow potentials)	500 ms
Robitaille et al., 2010	200 ms	1000 ms	400-900 ms	300 ms
Delvenne et al., 2011	100 ms	900 ms	250-750 ms	250 ms
Mitchell & Cusack, 2011	150 ms	jittered between 900-1500 ms	330-530 ms	> 520 ms
Sander et al., 2011	100 ms	1000 ms	ca. 400-750 ms	350 ms
Sander et al., 2011	500 ms	1000 ms	ca. 450-700 ms	800 ms

[a]Dependent on age group; see text for further details.

Furthermore, a look on Figure 2 of Delvenne, Kaddour and Castronovo (2011) reveals that CDA amplitudes for different set sizes converge after about 750 ms after onset of the memory array (lateralized change detection task, 100 ms memory array, 900 ms retention interval). Also Mitchell & Cusack (2011) observed a memory load effect on CDA amplitude only in the earlier part (ca. 250-650 ms) of the retention interval (lateralized change detection task, 150 ms memory array, 900 – 1500 ms retention interval, see Figure 4A in Mitchell & Cusack, 2011). They discuss a lack of power as possible explanation for the missing set size effects near the end of the retention interval (only 7 participants). However, actually they do have a CDA-effect at the beginning of the retention interval and the question arises why power should suffice during the early but not during the late retention interval. Actually, the more transient nature of their CDA matches well our observations and might remain even when data from more participants are added. There is a further study with a rather narrow CDA-window. Sander et al. (2011) observed set size effects on CDA amplitude only from about 400-750 ms (lateralized change detection task, 100 ms memory array, 1000 ms retention interval). See Table 17.1 for an overview.

Interestingly, the study of Sander et al. (2011) adds a further critical aspect concerning the duration of the CDA. They examined three age groups—children, younger adults and older adults—and the exact time window they choose for analysis differed somewhat for the three groups. Furthermore, they additionally run a condition with a memory array of 500 ms and this manipulation led to a shift and decrease in size of the CDA-time window for all three groups. In particular, the time window started later and ended earlier as compared to the 100 ms memory array for all three groups (Sander et al., 2011, Table 2 for the exact times for CDA analysis in all conditions). Contrary, in a study conducted in Vogel’s lab, comparing younger and older adults, these differences in the durability of the set size effect in CDA amplitudes were absent. Both age groups elicited a CDA starting about 300 ms after the onset of the memory array and lasting until the end of the retention period (Jost et al., 2011).

Taken together, there is considerable variation in the duration of the set size effect in CDA amplitudes between experiments, even when nearly completely the same design was employed. In experiments of the working group of Vogel the CDA is truly sustained in nature, whereas most other researchers—just like we—observe a more transient component.

Methodological differences

One possible explanation for the observed transient nature of delay activity in several studies is methodological in nature. The filtering out of slow drift artifacts during recording might involuntarily have eliminated part of the slow potential activity in some studies. Indeed, the various studies employed different low-cutoff filters (Vogel-Lab: .01 Hz; Sander et al., 2011: 0.5 Hz; Mitchell & Cusack: .003 Hz; Robitaille et al. 2009, 2010: N/A; Delvenne et al., 2011: .01 Hz; our experiments: .016 Hz). However, a comparison with Table 17.1 shows that there is no systematic relationship between the employed low-cutoff filters and the duration of load-effects in the CDA. As the filter’s roll-off is usually not reported, we cannot compare for this potential influence. If it will turn out that no methodological differences cause the variability of duration of load-effects in the CDA, what cognitive explanations might account for this variability?

Anticipation of test array

Another explanation takes into account, that already after several trials, participants get a feeling for the duration of the retention interval. In other words, they can more or less gauge the duration of the retention period and hence anticipate the onset of the test array. This anticipation of the test array and the preparation for the comparison of the retained information and the subsequent response might change the format or the state of the held representation. Maybe the representation changes from a state of more passive storage into an active state for the upcoming comparison with the test array. Interestingly, in line with this reasoning, Vogel and colleagues (McCollough et al., 2007; Perez & Vogel, 2011) reported that the strength of the CDA diminishes near the end of the retention interval. This diminution of the CDA goes back to an increase in ipsilateral delay activity, which the authors discuss as potentially reflecting anticipation processes for the upcoming test array (McCollough et al., 2007). Please note, that we also observed a modulation of ipsilateral slow potentials as a function of set size in the last section of the retention interval in Experiment 2 that was not explainable in terms of maintenance processes (see Chapter 6.4).

To test the anticipation-hypothesis one might design a version of the lateralized change detection task with a retention interval randomly varied in length. The set size effect in the CDA might not vanish towards the end of the retention interval, when participants cannot foresee the onset of the test array. However, we have to keep in mind that Vogel and colleagues do find a sustained CDA until the end of the recording epoch. If the anticipation-hypothesis is right, it additionally has to explain why there are these differences in the duration of the CDA between experiments and especially between research groups. Maybe slight task differences or slightly different foci in the instruction of the participants account for these discrepancies of results.

Consolidation into visual working memory

A further, but until now wholly unsubstantiated, hypothesis is that the posterior slow potential and CDA activity actually does not reflect the maintenance of items in visual WM, but rather only the entrance and consolidation into visual WM. In this function, their duration would not have to span the complete retention interval. Interestingly, in the face of the consolidation-hypothesis, Sander et al.'s (2011) observed variations in the durability of the set size effect in the CDA for different age groups might be reinterpreted. The duration of the set size effect is shortest for young adults as compared to children and older adults (Sander et al., 2011). Maybe, these variations actually mirror differences in consolidation efficiency.

To conclude, obviously there are considerable differences in the duration of load effects on CDA amplitude between experiments. Why they are there is not so easy to say. The critical point is that, if these differences are not due to methodological reasons, as for example different employed filters, the CDA does not span the whole retention interval in many experiments. This is actually incompatible with the idea of delay activity that it carries object information until the test array is shown. Further research is necessary to decide if, on the one hand, the CDA truly mirrors maintenance processes and that these processes change near the end of the retention period when participants prepare their answer in anticipation of the test array, or if, on the other hand, the CDA actually mirrors other processes, maybe the consolidation into visual WM.

18 Plasticity of Visual Working Memory

One main topic of the current dissertation project is the question whether visual WM is susceptible of change. Notably, short-term modifications of WM performance have to be dissociated from more fundamental changes in WM efficiency.

There exist large interindividual differences in WM capacity (e.g., Engle et al., 1999; Vogel & Machizawa, 2004). In addition, there are intraindividual differences in measured visual WM capacity. Measured WM capacity depends on variables such as sleep deprivation and fatigue, drug consum and stress (for a review, see Engle, 2010). This is clear indication that WM efficiency of a person is not completely stable and depends to some degree on transient external influences. Incentives constitute such a short-term influence of a person’s state. They can induce a state in which participants concentrate better and invest more effort to the task. Although results reported in the literature are mixed (see Chapter 5.1 for a review), we observed clear incentive effects. Participants’ increased effort was reflected in improved visual WM performance as well as in altered electrophysiological activity (see Experiment 1).

However, even though measured WM efficiency depends on a person’s current state, it is not infinitely improvable through factors like effort or arousal. Measured WM efficiency is also determined by personal limitations in the amount of the underlying neuronal resource, that is, the available capacity. Therefore, dependent on the vantage point visual WM can be considered both a stable trait as well as a transient state (for a similar discussion see Engle, 2010). As WM seems to play a crucial role for higher cognition, the question whether WM capacity of a person can be improved has attracted much scientific scrutiny. Training studies are a useful tool to investigate this question. In contrast to short-term modifications of WM efficiency, as for example incentives, WM training aims for more than just setting a person in a more concentrated state. Via training stable long-term improvements of persons' WM processes shall be achieved. That is, via training WM efficiency as a trait shall be improved. For this reason, the validation of long-lasting training effects constitutes an important part of training studies (see Chapter 8.1.4 for a review).

We observed behavioral effects of improved visual WM efficiency for both, short-term modifications (Experiment 1) as well as training interventions (Experiment 3). Furthermore, we showed that electrophysiological components of visual WM are also sensitive to both forms of interventions. Posterior slow potentials increased in amplitude under incentives in Experiment 1, indicating that participants invested more effort and maintained more information as compared to the baseline condition. Furthermore, in Experiment 3, the pattern of contralateral slow potentials' amplitudes indicated that filtering efficiency in visual WM increased from pre to post training session. These plasticity effects in visual WM were reflected by posterior slow potentials, but not by the CDA. The bottom line is that according to our results, contralateral slow potentials, but not the CDA, are suitable measures of plasticity in visual WM efficiency.

19 Reconsidering Selection Mechanisms

19.1 Types of Selection Mechanisms

We have built the training study on the plausible assumption that the MOT as well as the change detection task with distractors necessitate sustained attention towards targets and prevention of attentional capture through distractors. Although training of filter ability in MOT was efficient, there was no transfer to improved selection mechanisms to the change detection task. These results are strong indication that sustained attention towards targets and away from distractors is not the crucial selection mechanism in the change detection task. Therefore, we now examine again the attentional processes running during initial selection. Critically, the exact design of the change detection task with distractors might determine which attentional processes are at work during initial selection. Based on these considerations, in Chapter 19.2, we will further discuss why we might not have observed transfer effects and develop a new hypothesis about filtering in the change detection task as employed in our training study.

During the memory array of the change detection task with distractors there are two classes of stimuli, targets and distractors and participants have to select the targets for maintenance in visual WM and reject the distractors. In the particular design employed in Experiment 3, participants performed a *feature-based selection* according to shape; they had to select the squares out of the rectangles (as in Fukuda & Vogel, 2009). In the literature, there exist further designs with other criteria how to select the targets out of the distractors (see Figure 19.1 for an overview). Vogel et al. (2005) also employed a feature-based selection and defined the color of the items as selection criterion; red items were targets, blue items were distractors. In a further experiment of their study, participants selected the targets based on their location, not on their features (Vogel et al., 2005). Shortly before the presentation of the memory array, a central arrow pointed towards the upper or the lower quadrant of the relevant display side. The items in the indicated quadrant were defined as targets, the items in the other quadrant as the distractors. A further example for a change detection design with a *location-based selection* criterion, is the study of Herrero, Nikolaev, Raffone and van Leeuwen (2009). They employed a spatial cueing of each individual target. Shortly before the appearance of the memory array frames appeared at the target locations but not at the distractor locations. In a further version of the change detection task with distractors, distractors were marked to enable participants to prepare for ignoring them (Herrero, Crawley, van Leeuwen & Raffone, 2007). This was done by presenting a preview array shortly before the appearance of the memory array. This preview contained only the later distractors and importantly the distractors were presented at the same location as in the memory array. Participants could thus use the preview to prepare which object locations to neglect in the following memory array. Actually, different selection criterions demand different selection processes. Therefore, we now have a closer look on how the choice of the selection criterion determines the process of selection.

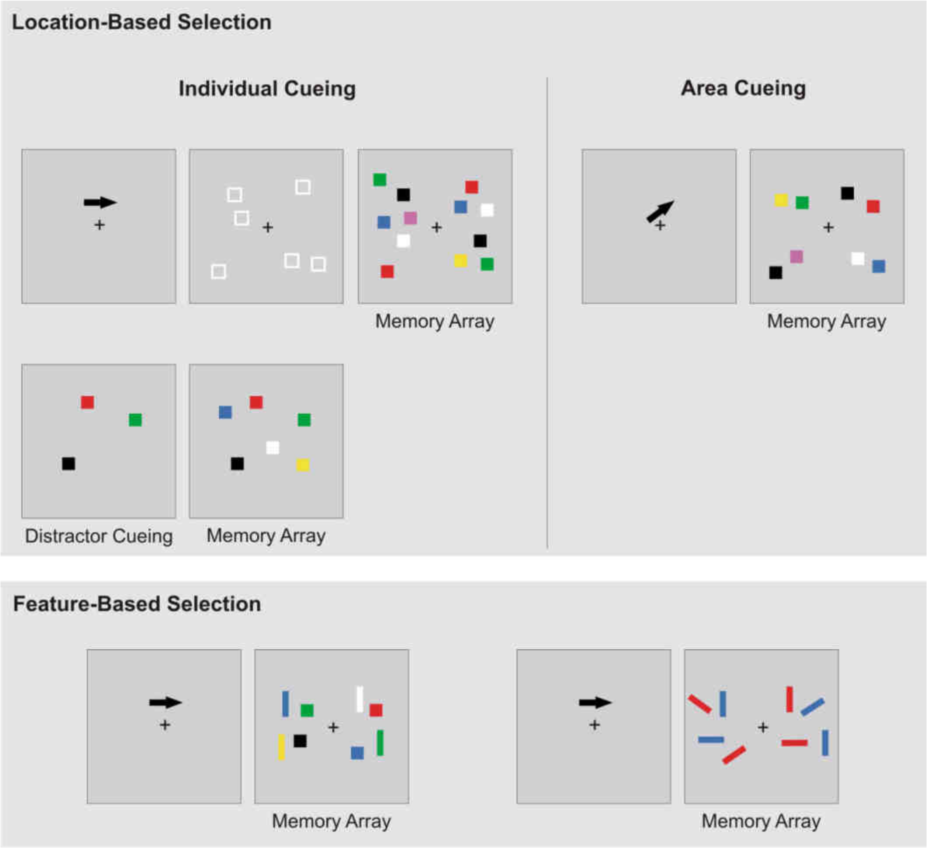

Figure 19.1. Classification of different selection criteria in the change detection task as employed in the literature.

There are two broad classes of selection criteria employed in the change detection task with distractors, selection based on location and selection based on features (see Figure 19.1). Selection based on location can be subdivided into (a) *area cueing* (e.g., the quadrant of the display, Vogel et al., 2005), (b) *cueing of individual target locations* (Herrero et al., 2009) and (c) *cueing of individual distractor locations* (Herrero et al., 2007). The word "cueing" already focuses on the crucial difference between selection based on features and selection based on location. In the latter case, relevant locations are cued prior to memory array onset and therefore spatial attention is already oriented away from the distractor locations. In (a) it dwells in the area where the targets appear and in (b) it is even at the precise target location when targets appear. In (c) locations of distractors might already be inhibited. This constitutes an early selection mechanism based on spatial locations only. Contrary, in the case of feature-based selection, all items have to be processed to a certain degree to differentiate between targets and distractors. In that case, selection can only start after onset of the memory array and an initial allocation of attention towards each item is needed.

Actually, there seems to be some variation in the difficulty of the types of selection. Location-based selection—at least in the case of area cueing—seems to be easier then feature-based selection. A comparison of Figure 1b and 2b of Vogel et al. (2005) reveals, that poor filterers are completely unable to filter out the irrelevant distractors in the case of object-based selection as indicated by an equal CDA amplitude for high-memory load and distractor-present conditions. Contrary, in the case of location-based selection, poor filterers seem to be able to filter at least some of the distracting information, as indicated by a CDA amplitude for the distractor-present condition that lies in between the low and the high-memory load conditions (for a detailed description of Vogel et al.'s design, see Chapter 7.1).

Actually, the lateralized change detection task by itself also contains distractors, namely the items in the irrelevant hemifield. In this task area cueing is employed to induce a location-based selection. Specifically, the targets can be selected via a central spatial cue indicating the relevant hemifield. In Experiment 2, ipsilateral slow potential activity indicated a processing of irrelevant items when only one relevant item was present, indicating that in this case these irrelevant items were not filtered out. However, a relationship between the extent of filtering and visual WM capacity as reported in Vogel et al. (2005) was not observed. Filtering within one hemisphere might necessitate a more sophisticated filter mechanism, a mechanism possibly more strongly related to working memory capacity.

To conclude, the choice of the exact selection design in the change detection task might have important implications concerning the exact types of attentional processes at play. Backed with this knowledge we now attempt to figure out why the MOT training did not transfer to the change detection task.

19.2 Truly Attentional Capture?

We designed our training study based on the results of Fukuda and Vogel (2009). These authors report that distractors involuntary capture the attention of poor filterers in a lateralized change detection task (see Chapter 7.2). Therefore, a training of attentional control in the presence of distractors seemed to be indicated to improve their selection mechanisms and hence, we have chosen the MOT task as training task. In this task, participants trained to hold attention sustained on the targets and to prevent attentional capture through distractors. In the following, we outline that maybe we observed no transfer effects, because attentional capture through distractors is actually *not* the critical process that leads to poor filtering in the change detection task with distractors.

Maybe, Fukuda and Vogel’s (2009) application of the attentional capture explanation to the change detection task with distractors was premature. They might have adopted this explanation because it was most probably true for another experiment of their study. In this other experiment four Landolt “C”s were presented on the screen. These Landolt “C”s only differed in the side where their gap was located. Shortly before their appearance, one of the four Landolt “C”s, the target, was spatially cued via a green dot at its exact location; the other three Landolt “C”s constituted the distractors. Participants’ task was to indicate the side of the gap in the target. Employing the dot probe technique, the authors showed that participants differed in where they allocated their attention shortly after the Landolt “C”s disappeared. High-capacity participants focused their attention towards the target, whereas low-capacity participants dwelled with an equal probability with their attention on the target or the distractors. The authors conclude that low-capacity subjects have been more prone to the distractor-Landolt “C”s, because—additionally to the target-Landolt “C”—they also involuntarily captured their attention. Contrary, high-capacity subjects were able to resist attentional capture.

However, that the same selection process contributes to the change detection task with distractors and the task with the Landolt “C”s, as assumed by Fukuda and Vogel (2009) is, however, not necessarily true. In the preceding chapter, we differentiated between two selection mechanisms, selection based on features and selection based on location. The latter was also employed in the experiment of Fukuda and Vogel (2009) in which the side of the gap in the target Landolt “C” has to be detected. The relevant target location is exactly cued and hence an early selection based on location is possible, prior to the objects’ appearance. Consequently, there is absolutely no need for participants to shift attention towards the distractor objects. The susceptibility of participants with low WM capacity to nevertheless allocate attention towards distractors indicates that distractors have involuntarily captured their attention. Contrary, in the change detection task, that Fukuda and Vogel (2009) as well as we employed, targets and distractors have to be discriminated based on their features. This implies that all objects have to be processed to a certain degree to differentiate between targets and distractors. However, when *all* participants *have* to process the distractors to a certain degree to decide that they are distractors, there cannot be an attentional capture through distractors.

Interestingly, in a recently published study, the authors (Fukuda and Vogel, 2011) showed that actually all subjects are susceptible to attentional capture, but only differ in the time needed to recover. This is actually a further indication that attentional capture is not the crucial process that makes filtering difficult in a change detection task where distractors have to be filtered out based on their features. If, as Fukuda and Vogel (2011) showed, all participants can recover from attentional capture, why should they store the distractors later on in their visual WM? However, this is exactly what Vogel and colleagues (Vogel et al., 2005; Fukuda & Vogel, 2009) as well as we observed: Poor filterer store more unnecessary information in their visual WM.

However, if not attentional capture, what might be an explanation for the data pattern observed by Fukuda and Vogel (2009). Employing the dot probe technique the authors showed that shortly after memory array offset good filterers allocate their attention exclusively on the targets, whereas poor filterers also dwell on the distractors. Under conditions of feature-based selection, as in the change detection task employed by these authors, all items have to be processed to a certain degree. When the items are processed thus far that targets and distractors can be dissociated, the distractors can be dropped again. Maybe, good filterers are better in the disengagement of attention from the distractors as compared to poor filterers. The latter participants might not be able to drop the distractors and hence bind their limited resources for the further processing of these distractors. This would also explain why these distractors later on occupy visual WM (Fukuda & Vogel, 2009; Vogel et al., 2005; Experiment 3 of the current work).

Coming back to our training design, interindividual differences in susceptibility to attentional capture might not account for differences in filter ability in a change detection task in which distractors have to be filtered out based on their features. This might explain the missing transfer effect in our training study, albeit clear training gains in filtering efficiency in the training task (MOT). Furthermore, in MOT participants trained to hold their sustained attention on targets. If the interindividual differences in filter ability actually go back to interindividual differences in the efficiency of attentional disengagement from initially included distractors, a training of sustained attention towards targets and avoiding attentional capture of indistinguishable distractors—as needed in MOT—cannot work. Fukuda and Vogel (2009) showed that good filterers are able to drop the targets already 50 ms after memory array offset. Hence, a training should target the processes in that early time interval. One might train participants' efficiency in selecting the relevant information and dropping the distractors as soon as they have processed the items far enough to differentiate between targets and distractors.

19.3 Searching Targets

Imagine you are searching for a specific pen in a pencil case. In that case you are searching for a specific object in the presence of similar ones and without knowing its location. This is exactly what can be investigated via visual search paradigms. They are useful tools to measure the efficiency of attentional allocation and attentional selection in vision. Participants see several objects on the display and a commonly used task instruction is to decide as fast as possible if a given target is present in the display or not (for example a vertical line in the presence of lines with other orientations). There are remarkable similarities in task affordances between the visual search paradigm and the change detection task with distractors as employed in Experiment 3. In particular, the memory array of the change detection task constitutes a visual search display with targets intermingled with distractors. Hence, the accumulated knowledge about processes running during visual search can assist in strengthening our understanding of the processes going on during initial selection of targets into visual WM.

19.3.1 Pop out versus serial search

There are two typical result patterns for visual search. Firstly, the target can constitute a singleton, that means a target outstanding in terms of its features. If that is the case, detection times are very fast and independent of the number of distractors, for example a red target bar under blue distractor bars (pop out; Treisman, 1986). Secondly, if there is no pop out, the more items are presented on the screen, the longer it takes the participant to detect the presence of the target (Schneider & Shiffrin, 1977) because the display has to be searched more intensively for the items. Contemporary models of visual search assume that this search might be a combination of serial and parallel search (for a review, see Wolfe, Vo, Evans & Greene, 2011). A pop out occurs if the target is categorically different from the distractor (Eimer & Kiss, 2010; Wolfe et al., 1992), for example a red among blue items or a diamond among circles or a horizontal bar among vertical ones. Additionally, a pop out occurs if the target and the distractors are on different poles of a continuum (for a review, see Soto, Hodsoll, Rotshtein & Humphreys, 2008), for example a small item among large ones. There is no pop out if targets are defined as a combination of two or more features, as for example color and shape, and some distractors share the one and other distractors the other feature with the target (Treisman, 1986). There is also no pop out, if more than one search template is task-relevant, as when participants have to look for red and green targets among blue distractors (for reviews, see Olivers, Peters, Houtkamp & Roelfsema, 2011; Soto et al., 2008).

This has important implications concerning the design of the memory array of the change detection task. If the targets pop out, encoding time should be shorter as if, on the other hand, the display has to be searched for the targets. This was shown in a combined visual search and change detection design (Mayer et al., 2007). The memory array constituted of a 3 × 3 grid of nine grey shapes and between one up to five of these shapes (targets) had to be maintained in visual WM. The remaining shapes constituted distractors. Targets had to be searched for via visual search. In that way, the memory display of the change detection task constituted a visual search array. Visual search was either easy due to a pop out of the targets or difficult without target-pop out. Participants indicated via key press when they had finished encoding of targets. The exact same shapes were shown in both conditions. Although exactly the same targets had to be encoded into visual WM under both conditions, required encoding time was significantly longer for the condition without target-pop out as compared to the pop out condition (Mayer et al., 2007). This is clear indication that a pop out of targets facilitates encoding into visual WM. Please note that even in the pop out condition, encoding time was a function of the number of to-be-encoded items. This might be due to the fact that although the pop out facilitated target *detection*, the subsequent *processing* of target information for storage in memory depends on the amount of to-be-encoded information.

19.3.2 Two steps during encoding

The observation of Mayer et al. (2007)—that even when targets pop out, encoding time into visual WM is dependent on the number of targets—leads to an important difference between most visual search experiments and the change detection task with distractors. The task-goal during most visual search tasks is to detect a target out of distractors. Participants only have to indicate if the target was there or not. During change detection, additionally to the detection of the targets, a further step is necessary to solve the task, namely the identification of the to-be-remembered feature of the targets. In the change detection task we employed in Experiment 3, as a first step squares had to be detected out of rectangles (*visual search*) and as a second step the color of each square had to be identified for later maintenance (*feature pick up*).

Interestingly, Fukuda and Vogel (2011) employed a visual search design where exactly these two steps have to be performed. Participants had to report the location of a gap in one of four presented Landolt "C"s. The target Landolt "C" was defined via its color. Participants consequently first had to search for the target and then to pick up the critical feature. Initially after the disappearance of the search array a mask was presented. To equate performance accuracies to about 75%, the authors determined the individual presentation time of the search array for each participant; presentation times ranged from 35-183 ms for a performance accuracy of about 75%[4]. This illustrates impressively that persons strongly differ in their efficiency to detect task-relevant information in a visual-search display where they have to perform the two steps of searching the relevant target and additionally picking up the relevant feature within this target.

The observation that there exist huge interindividual differences in the time needed to search the relevant targets and to additionally pick up the-to-be remembered features has important implications for the interpretation of interindividual differences in visual WM performance in the change detection task with distractors. As the memory array is often presented for a very short time (100 ms in our experiments) not all participants might be able to search

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[4] Please note that we here refer to the baseline condition of the experiment of Fukuda and Vogel (2011).

through the items and pick up the relevant target information before the memory array disappears. Therefore, part of the interindividual differences in performance accuracy in the change detection task might actually be driven by interindividual differences in the efficiency to search trough and pick up item information. As these two steps might actually be considered the process of consolidation of relevant item information under distraction, its further investigation might benefit from techniques employed in the investigation of visual WM consolidation (e.g., Sun, Zimmer & Fu, 2011; Vogel, Woodman & Luck, 2006). Especially, to gain complete control over encoding times, the memory array should be masked as done in Fukuda and Vogel (2009).

19.3.3 Parametrical manipulation of target-distractor similarity

Weidner, Krummenacher, Reimann, Müller and Fink (2008) parametrically varied the similarity of a target and distractors in a visual search task. They observed that the more the target resembled the distractors, the more time was needed to detect the target[5]

If, however, the presentation time is fixed, error rates should increase with increasing similarity of targets and distractors. If targets subsequently have to be maintained in WM, as in the change detection task, this should also have impacts on response accuracies. In a preliminary experiment (that is not part of the dissertation project and therefore analyzes are not presented here) we varied within participants the aspect ratio of rectangles (distractors) to manipulate their similarity with squares (targets) in a change detection task. As usual, the presentation time of the memory array was 100 ms. Indeed, participants’ response accuracy was a function of the similarity of targets and distractors. The more the two stimulus classes differentiated and hence the better they could be discriminated, the better the WM performance accuracy during test.

The initial encoding of targets in the presence of distractors is a critical step in the change detection task with distractors. That the efficiency of initial encoding has influences on later memory maintenance processes is obvious. A deeper knowledge about what happens during encoding would prevent the intermingling of processing bottlenecks during encoding with maintenance processes during the retention interval. The available encoding time and the similarity of targets and distractors constitute two crucial parameters.

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[5] Interestingly, reaction times continuously increased with increasing target-distractor similarity, indicating that pop out is not an all-or-nothing phenomenon.

20 Sustained Attention during Visual Working Memory Maintenance

During the course of this thesis we repeatedly touched the construct of *attention* in the context of WM. In Experiment 2, for example, we explained the filtering out of irrelevant items with the construct of sustained selective attention towards the relevant items. Similarly, we assumed that the selection mechanism in Experiment 3 might be selective attention towards the relevant items. Moreover, we interpreted the frontal boost for distractor-present trials as a top-down elicited attentional control signal.

The constructs of attention and WM try both to explain the information processing—and its limits—in the service of behavioral goals. Attentional processes promote the efficient encoding of goal-related information in the presence of irrelevant sensory input, whereas WM processes guide the maintenance of a small amount of relevant information for further processing. By this means, both processes enhance the processing of relevant information in the presence of distracting information (for a similar discussion see Awh et al., 2006). Interestingly, both cognitive constructs mutually influence each other and seem to be closely intertwined (e.g., Awh et al., 2006; Cowan, 2001; Engle et al., 1999). In particular, a variety of studies emphasize the relationship between the ability to control attention and WM capacity (Bleckley, Durso, Crutchfield, Engle & Khanna, 2003; Kane et al., 2001; Sobel, Gerrie, Poole & Kane, 2007). Low-capacity subjects are less able as compared to high-capacity subjects to control their attentional allocation in various attention tasks, such as visual search tasks (Sobel et al., 2007), selective attention tasks (Bleckley et al., 2003) and antisaccade tasks (Kane et al., 2001).

Decades of research converge to a straightforward conclusion: Attention exerts strong influence on efficient WM functioning (e.g., Awh et al., 2006; Cowan, 2001; Engle et al., 1999). However, attention can guide WM in a variety of ways. It might play a crucial role at several stages for efficient working memory functioning: We already discussed its function as a gatekeeper into visual WM in the preceding chapter. Furthermore, it might contribute to successful maintenance in visual WM. Here, we focus on this latter function.

20.1 Attention as a Rehearsal Mechanism

In several WM-theories, the sustained allocation of attention towards the maintained information is assumed to be the cognitive mechanism that enables the maintenance of information in WM (e.g., Awh et al., 2006; Jonides, Lacey, Nee, 2005; Postle, 2006; Zimmer, 2008). Most theoretical underpinning of this idea is guided by the attentional-rehearsal theory of Awh and colleagues (e.g., Awh & Jonides, 2001; Awh et al., 2006). In Experiment 2, we reasoned that biased attention towards the items in the relevant hemifield might be the mechanism that enhanced the processing of these relevant items in the presence of distractors (see Chapter 6.4). Here too, we applied the attentional-rehearsal theory.

In this theory, Awh and colleagues developed the idea that sustained spatial attention is the rehearsal mechanism for maintaining information in spatial WM. They collected converging evidence for their theory. Firstly, spatial WM and spatial selective attention elicit activity in strongly overlapping frontal and parietal brain regions (Awh & Jonides, 1998). Secondly, the authors compared electrophysiological responses to shortly appearing probes in an attention task and during the retention interval of a spatial WM task. Probes at attended and remembered positions elicited components with highly similar latency and topography (Awh, Anllo-Vento & Hillyard, 2000). Thirdly, Awh and Jonides (1998) showed that stimuli presented at to-be-memorized locations are processed faster than stimuli at irrelevant, not to-be-memorized locations, indicating that attention towards the to-be-memorized locations is crucial for spatial WM maintenance. As a main task, their participants had to remember the identity or the location of a letter in WM. A probe stimulus was presented during the retention interval—either at the same location as the letter or at another location—and participants' secondary task was to react as fast as possible upon that probe. In the spatial condition, participants' reaction times to the probe were faster if the probe appeared on the to-be-memorized location as compared to irrelevant locations. There was no difference in response time towards the probe when the identity of the letter had to be memorized. Fourthly, Awh and Jonides (1998) found that interruptions of attentional allocation during the maintenance interval led to declines in WM performance, indicating a functional role of attention during spatial WM maintenance. In a dual-task design, their participants performed a spatial change detection task in which they had to remember a single location. During the maintenance interval, a colored stimulus was presented and subjects had to indicate its color. In one condition, participants had to reallocate attention away from the memorized location in order to indicate the color of the stimulus, whereas in the other condition this was possible without shifting their attention away from the memorized location. Performance in the spatial change detection task was better, if no spatial reallocation was necessary.

However, this truly constitutes a spatial mechanism for the maintenance of location information and hence this is not directly applicable for the maintenance of visual information in visual WM. In the visual change detection task for objects not only spatial information about the objects has to be maintained during the retention interval, but feature information of the objects, as their color, shape or orientation. Also for the maintenance of object information an attentional mechanism can be postulated, but we require a careful characterization how this visual mechanism might work.

Actually, considering Awh’s research on a spatial based attentional rehearsal mechanism might help to develop a corresponding rehearsal mechanism for object or feature information. In particular, part of his research on attentional mechanisms for spatial WM might be transferred towards the object domain. One part of his evidence constitutes overlapping neuronal areas between vision and WM. Indeed, recent research has presented first evidence for delay activity during visual WM maintenance highly specific for specific features, such as color or orientation (Harrison & Tong, 2009; Serences, Ester, Vogel & Awh, 2009). Crucially, this delay activity was found in primary visual areas V1-V4 (Harrison & Tong, 2009; Serences et al., 2009), known to comprise neurons sensitive for colors, orientations, edges, etc. Furthermore, Serences et al. (2009) found highly overlapping patterns of activity during visual WM maintenance and sensory processing of stimuli. The sustained activity in primary visual areas observed during WM maintenance might constitute a rehearsal mechanism for the respective feature information.

The specific task we used to examine visual WM was the change detection task. Interestingly, the memory array of this task contains feature information about the to-be-remembered objects as well as information about their spatial locations. In the next chapter we discuss which of the here discussed processes of sustained attention might contribute to maintenance in the change detection task. In particular we ask which of these attentional processes are reflected in the CDA.

20.2 The Role of the CDA

In the lateralized change detection task, multiple objects have to be maintained in memory. In each trial, several objects are distributed randomly throughout a specified array so that their exact location and configuration cannot be foreseen by the participants. Spatial attention towards the targets might play a crucial role during maintenance. Already when introducing the CDA, we mentioned their potential role as a spatial pointer (e.g., Drew et al., 2011; McCollough et al., 2007) towards the objects during the retention interval of the lateralized change detection task as well as during a lateralized MOT task (see Chapter 4.3). The posterior IPS is discussed as the neuronal source underlying this spatial pointer mechanism (e.g., Drew et al., 2011; see Chapter 4.4).

Decades of research have shown that spatial attention can be directed towards individual objects. Contrary, many early attentional theories assumed that attention functions as a kind of spotlight that illuminates everything within the attended region of space. The boundaries of attention were defined as the spatial extent of the spotlight. However, it has been shown that there is a crucial relationship between the focus of attention and the stimuli in the visual scene the observer is attending to. That objects rather than locations can guide attentional allocation implies that attentional allocation is not defined through a specific region in space, but through the boundaries of objects (for a review see Scholl, 2001). In line with this reasoning, the existence of split attentional foci, directed specifically to objects allocated throughout the display, has been shown (Awh & Pashler, 2000). Moreover, the direct surrounding of an attended object is attentionally inhibited (Hopf et al., 2006). Further support for the object-based attention account comes from studies that showed that attention is spreading automatically throughout the selected object (e.g., Ahw, et al., 2001; Duncan, 1984). To sum up, objects seem to constitute discrete units to which spatial attention is directed.

There are several hints that bolster the supposition of spatial attention towards the object locations also during visual WM maintenance. In the introduction we already reviewed evidence that the removal of context information (Jiang et al., 2000) or a change of the spatial arrangement (Zimmer & Lehnert, 2006) disturbs, even when completely irrelevant, the performance in change detection of feature information. These results converge to the view that the spatial configuration promotes WM maintenance for feature information. Theeuwes, Kramer and Irwin (2011) used the dot probe technique to learn more about the contribution of spatial attention during a change detection task for colored stimuli. After the retention interval, they asked their participants if a specific color was among the remembered items, for example “red?”. Shortly afterwards, in some trials a dot appeared at any of the locations of the to-be-remembered stimuli. Participants’ task was to respond as fast as possible and only after this, to answer the memory-question, if that specific color was among the to-be-remembered stimuli. The crucial result was that, when the dot appeared at the specific location, the participants were retrieving to answer the memory-question, reaction times towards the dot were increased as compared to when the dot appeared at the location of any of the other stimuli. Taken together, spatial information about the object locations seems to play a crucial role during visual WM maintenance.

The exact pointing towards the relevant locations might be especially relevant in case of additional distracting information, as in the change detection task with distractors. Fukuda and Vogel (2009) already showed with the aid of the dot probe technique that poor filterer allocated their attention more often towards distractor locations, whereas good filterer focused their attention towards target locations. However, they presented the dots already 50 ms after the memory array, shortly after the time of perceiving the objects and well within the scope of iconic memory. It would be highly interesting to employ the same technique, but at different times during the retention interval to learn about the attention allocation during maintenance in visual WM. We would predict that the pattern remains the same as the one Fukuda and Vogel (2009) observed, namely that good filterer can focus their sustained internal attention towards the target locations throughout the retention period whereas poor filterer cannot.

However, only knowing about the locations of the to-be-remembered objects in a change detection task does not allow for the detection of a potential feature change, such as color or orientation. As already discussed in the preceding chapter, only a spatial pointer mechanism as assumed for spatial WM (e.g., Awh & Jonides, 2001) is not enough for the maintenance of visual information, there must additionally be a mechanism for the maintenance of the feature information. We now have a closer look on how both processes, the maintenance of location-information as well as of feature-information might contribute to successful visual WM and further discuss the possible role for the CDA[6].

What might be the role of the CDA? It might exclusively reflect a spatial pointer towards the target locations or it might additionally hold some of the objects' features (cf., McCollough et al., 2007). There is evidence that the CDA does not reflect the size of an attentional zoom lense (McCollough et al., 2007), that the CDA does not depend on the perceptual requirements (Ikkai et al., 2010; Luria et al., 2010) and that the CDA does not simply reflect the number of locations that are covered by objects (Ikkai et al., 2010; see Chapter 4.1 for a detailed presentation of these experiments). All these data converge to the straightforward view that the CDA indeed is a measure of the number of representations in visual WM. Crucially, however, not any of these studies allows for statements about the question whether the CDA does reflect the processing of any *features* of these objects. Also in the study of Luria and Vogel (2010) no evidence is provided for the assumption that the CDA might be sensitive for feature information of the stored objects (cf. Chapter 4.3). They discuss their CDA patterns as indication that bound-objects are stored in visual WM. However, as already discussed in Chapter 4.3, their results are also to be expected when the CDA reflects only a spatial pointer that is not sensitive for feature information of the represented objects. The only indication that the CDA might indeed hold some content information comes from Woodman and Vogel (2008), who report a larger CDA amplitude for the maintenance of orientation information as compared to the maintenance of color information of the very same stimuli (see Chapter 4.3).

How could the question whether the CDA is or is not sensitive for object content be further investigated? One might think of a research line related to the CDA research. Slow potentials measured in a standard, not lateralized version of the change detection task differ in topography based on the type of memorized information. In particular, slow potentials arising when maintaining spatial information have been dissociated from those arising when maintaining object information (e.g. Mecklinger & Pfeifer, 1996; Mecklinger & Müller, 1996). This indicates that—at least part of—the content of the memoranda is represented by

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[6] Concerning these questions much research focuses on the CDA. However, as we discussed (Chapter 17) the posterior slow potentials should not only be considered a building block of the CDA, but might contain relevant information beyond the CDA. Therefore, all following discussion equally applies to posterior slow potentials. To allow for a smooth reading, we only refer to the CDA in the following.

these slow potentials. When the CDA also codes part of the content of to-be-remembered objects, their topography should—comparable to these slow potentials—vary with the type of information. First indication that this is not the case is the study of Drew et al. (2011). They observed a CDA for a change detection task for colors as well as for a spatial MOT task. The CDA in the MOT task was more pronounced as compared to the CDA in the change detection task. The both tasks' common part of the CDA was equally distributed and its amplitude differed as a function of remembered or tracked items. This common part was interpreted to rely on the posterior IPS and reflect a spatial pointer towards the objects (see Chapter 4.3 for the discussion of the additional part of the CDA). This is first evidence that the CDA might not be sensitive for the content of the memoranda.

However, as already discussed above, in case that the CDA does not reflect the maintenance of to-be-remembered feature information, there must be another mechanism for its maintenance during retention. This brings us back to the in the preceding chapter discussed observations of sustained activity in primary visual areas (V1-V4) (Harrison & Tong, 2009; Serences et al., 2009). This activity is highly specific for the exact sensory information (Harrison & Tong, 2009; Serences et al., 2009). However, in case that the CDA reflects a spatial pointer towards and the object-content is stored in the primary visual areas, there must be any form of connection between these two. Maybe the CDA works as a coordinator that interacts with these sensory areas. It might constitute a pointer system that binds core object files via sustained attention at their locations and coordinates the processing in sensory areas. In that way, each stored feature would be assignable to a specific location and confusions would be prevented. This might actually be the reason for the observation that changing the spatial configuration in a change detection task disturbs the maintenance performance for shapes (Zimmer & Lehnert, 2006). When features are bound at locations to hold them individuated, features emerging at the "wrong" locations in the test array would consequently result in a mismatch with the maintained representation.

Interestingly, some theoretical accounts ascribe the spatial attention towards object locations a crucial role in the binding of several object features. Interesting in this context is Treisman's theory of binding object files during perception (e.g.; Treisman & Gelade, 1980; Treisman & Zhang, 2006) as well as during visual WM maintenance (Wheeler & Treisman, 2002). Remembering various objects with several features poses our brain the problem not to confound these features. The assignment of features towards the correct object—in other words the generation of bound object-files—is, according to Treisman and Zhang (2006), done via spatial attention towards the object locations. This sustained attention might also serve as the binding process during WM (Wheeler & Treisman, 2002). Highly interesting in the focus of this theoretical account, Fougnie and Marois (2009) showed that sustained attention during a change detection task is highly relevant for maintaining feature conjunctions and that a disruption of the attention during the retention interval impairs visual WM more for feature conjunctions as compared to individual features. The theory of Treisman goes hand in hand with an important theoretical account of Chun (2011). He reasons that parietal regions like the IPS (a favorite candidate for CDA generation) might not be the exclusive storage sides for WM information. Contrary, their role might be the direction of sustained attention towards the sensory regions that process the relevant feature information. Furthermore, he discusses a possible binding function of these regions—via sustained attention and in the sense of Treisman—during WM maintenance (Chun, 2011). In line with this reasoning, in case, that objects consisting of several features have to be maintained in visual WM, the CDA might bind these features together to an integrated object-file at specific locations during maintenance.

The CDA might even crystallize out to reflect some kind of domain-general attentional resource that is limited in capacity and works in the service of maintaining relevant information in an active state. This might be done via interactions between this cognitive resource and the sensory systems responsible for the storage of the respective content. A first step in investigating this question constitutes the just described study of Drew et al. (2011) that observed an equal CDA for spatial as well as feature information. Furthermore, one might design a change detection task for other to-be-remembered spatial information such as orientations as well as auditory information such as sounds at different locations. Obtaining a CDA in these designs as a function of the number of maintained spatial arrangements or as a function of the number of maintained sounds would be a first indication of at least some kind of domain-general functional role of the CDA. It might then constitute a capacity limited attentional resource that helps keeping entities individuated during the maintenance in visual WM via sustained attention towards their locations. However, these ideas are highly speculative and further research has to enlighten this question.

21 Conclusion

The first main issue of the present work was to gain a better understanding of the posterior slow potentials and CDA and their contribution to visual WM maintenance. Firstly, posterior slow potential activity crystallized out to be better in conformity with performance accuracies as compared to the CDA. This is also true for the observation of effects of visual WM plasticity. An incentive manipulation as well as a training of visual WM efficiency brought about performance improvements that were reflected in the posterior slow potentials, not in the CDA. Secondly, in all experiments we observed load-dependent ipsilateral delay activity that was interpreted to reflect, at least in parts, maintenance processes. This assumption is further supported by results from the literature. However, it is not yet clear, whether and under which circumstances they reflect the processing of the relevant or the irrelevant items. We outlined ideas for the further investigation of this topic. Based on this abundant empirical evidence, we arrive at the conclusion that contralateral as well as ipsilateral posterior slow potentials should not only be considered as the building blocks of the CDA. Instead, they reflect additional crucial processes of successful visual WM functioning that are subtracted out in the CDA.

Competent selection mechanisms are vital for efficient visual WM functioning. Our second main goal was the training of these selection mechanisms to enhance visual WM efficiency. We conclude that selection mechanisms in visual WM are improvable through training. This constitutes an enhancement of visual WM as a trait, as compared to variations in a person’s actual state for example via incentives as done in Experiment 1. However, we did not observe transfer effects from a training of attentional selection mechanisms in MOT to filtering in change detection. This indicated that the in the tasks employed forms of attentional selection are not equal. Specifically, we can exclude that the selection mechanism in the change detection task with distractors that we employed is the allocation of sustained attention towards targets and the prevention of attentional capture through distractors. To gain a deeper understanding of the specific attentional processes, we categorized selection criteria as employed in different change detection designs. We differentiated between early selection solely based on locations and late selection where irrelevant distractors have to be processed to some degree. These considerations are instructive for theories about selection in visual WM.

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