Costs and correlates of storage in visual working memory

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° ……………………………………………………………………Degree

η_p^2 ……………………………………………Effect size for ANOVAs (partial η^2)

ANOVA ……………………………………………………… Analysis of variance

CDA ………………………………………………Contralateral delay activity

cd/m^2 …………………………………………Candela per square meter

CDT ……………………………………………………Change detection task

cf. …………………………………………………………………Compare

CTI ………………………………………………………Cue-target interval

e.g. ……………………………………………………………For example

ERP ……………………………………………………Event-related potential

et al. ……………………………………………………………………Et alii

Hz ………………………………………………………………………Hertz

i.e. ………………………………………………………………………Id est

LC …………………………………………………………Locus coeruleus

ms …………………………………………………………………Milliseconds

mm ………………………………………………………………Millimeter

MSE ………………………………………………………… Mean square error

NE ………………………………………………………………Norepinphrine

p ……………………Probability of significance given that null hypothesis is true

SD …………………………………………………………Standard deviation

SPCN ……………………………… Sustained posterior contralateral negativity

VWM ……………………………………………………Visual working memory

Abstract

Visual working memory (VWM) refers to temporary storage of only a few items and it is intensely discussed how objects are represented. A less elaborated topic is how much effort is necessary to encode and maintain objects dependent on the type of task-relevant feature. In the first part of this dissertation project pupil sizes and event-related potentials (ERPs) were used to estimate storage effort during maintenance of visual information in change detection tasks (CDT) where set size and complexity of task-relevant features was manipulated. Either an easy feature (color) or a more complex feature (shape) of presented objects was task-relevant. We showed that pupil sizes indicate the number of stored objects and therefore can be interpreted to reflect attentional demands that are necessary to focus on presented stimuli. It could be further demonstrated that pupillary changes were independent of luminance effects of the presented stimuli. Slow potentials during retention were modulated by the type of task-relevant feature and were interpreted to reflect processing effort.

The second part of this work targets the question of how objects are represented in VWM by conducting a CDT where also task-irrelevant information was manipulated. According to object-based models items are always represented as integrated objects and the number of objects limits capacity in VWM. Feature-based models assume that the number and quality of features are the capacity limiting factors. Behavioral results revealed that changes of irrelevant information affect performance when color but not when shape was task-irrelevant. Nevertheless, in ERPs an irrelevant mismatch effect was found in both conditions and this effect was apparent until the respective individual capacity maximum for color and shape was achieved. We can conclude that features of presented objects in the current task were always represented independent of their task-relevance. These results were interpreted in terms of the VWM model provided by Brady et al. (2011) suggesting that objects are represented in hierarchical feature bundles which integrates object-based and feature-based VWM models.

Section 1
Storage in Visual Working Memory

1 Introduction into Visual Working Memory

According to Alan Baddeley (1992) “Working memory stands at the crossroads between memory, attention, and perception” (p. 559) and the underlying model outlines a system where a central executive is the hub between the visuospatial sketchpad and the phonological loop (Baddeley & Hitch, 1974). Whereas the phonological loop is responsible for temporary storage of auditory information, the visuospatial sketchpad can store visual information within a limited scope and time window. The central executive creates the connection between the subsystems and is involved in comparison processes between short-term memory and long-term memory as well as in directing attention i.e. to a specific task (Baddeley, 2003). Since 1974 a lot of research has targeted the visual component of this working memory model referring to the *visual working memory* (VWM). VWM is a temporary storage for only visual information that is highly limited in capacity and storage duration (Logie, Zucco, & Baddeley, 1990; Luck & Vogel, 1997). The following chapters explain in more detail the characteristics of VWM such as storage capacity, kind of object representation, or VWM assessment.

1.1 How to Measure Visual Working Memory?

When measuring the amount and quality of information that can be stored in VWM a lot of tasks cover different aspects of storage. N-back tasks are suitable to provide information about capacity of VWM. In these tasks participants are confronted with a series of sequentially presented stimuli either in visual, visuospatial or in auditory dimension. In 1-back tasks the current stimulus has to be compared with the previous presented item and participants are instructed to identify a match. The “N” can be replaced by an arbitrary number of trials and performance thus is assumed to reflect capacity of working memory. Nevertheless it has been shown that performance in N-back tasks is correlated with fluid intelligence which interferes with VWM capacity (e.g. Jaeggi, Buschkuehl, Perrig, & Meier, 2010).

A very well investigated method for estimating working memory capacity is the digit span task (cf. Miller, 1956). Several stimuli are presented sequentially in auditory or visual modality with the instruction to recall all stimuli afterwards. Difficulty in digit span tasks is manipulated via set size and item complexity. Span tasks usually interfere with reading and rehearsal processes since digits, letters, or words are used as stimuli. It is therefore difficult to instruct participants to recall visual objects which are not nameable. A visuospatial version of the span task refers to the Corsi-span task (Corsi, 1972), a block-tapping span task. Participants are required to remember a sequence of touched “blocks” and have to repeat this sequence afterwards. A suitable approach to estimate VWM capacity without interference such as verbal processes or fluid intelligence is the change detection task as explained in the following chapter.

1.1.1 Change Detection Task

Capacity limits in VWM are often investigated using change detection tasks (CDT) originally introduced by Luck and Vogel (1997). In this initial study a small set of objects was presented for 100 ms and after a 900 ms retention interval another set of objects appeared accompanied by the task to decide whether they remained the same or changed. In its simplest version colored squares were used and color was the task-relevant feature. Task difficulty was manipulated by presenting one to twelve differentially colored squares. Performance usually declines when three or four objects are presented (Luck & Vogel, 1997). To ensure that performance is not influenced by verbal rehearsal processes Luck and Vogel (1997) conducted a verbal load condition in their original study. The idea was that participants could verbally rehearse the colors during retention and thus improve their performance. Hence, participants additionally had to memorize 2 digits across each trial and say them aloud at the end. There was no alteration effect on performance in the verbal load compared to the no-load conditions. In the past years CDT was extended by creating objects with more different features such as orientation, size, or complex shapes (e.g. Eng, Chen, & Jiang, 2005; Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001) to further understand possibilities and limits of VWM.

A special case of CDT is the half-field paradigm where task-relevant stimuli are presented e.g. only on the right side of the screen and left-sided stimuli are considered as distractors (McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004). At the beginning of each trial a cue indicates whether the task-relevant information is on the left or the right side of the screen. Importantly, participants are not allowed to explore the study display but are instructed to only focus on the center of the screen. This version of CDT was constructed to investigate hemisphere-dependent electrophysiological correlates during processing of visual information and will be explained in more detail in the following chapter.

1.1.2 Electrophysiological Correlates and the CDA

Performance in VWM tasks reflects the match or mismatch of memory representations with the displayed material, though it provides no information about ongoing cognitive processes during the time course of maintenance. Therefore, to examine working memory retention, electrophysiological correlates, especially slow potentials, have been proven as suitable measure for working memory load in addition to behavioral measures (Rösler, Heil, & Röder, 1997; Rösler & Heil, 1991; Ruchkin, Johnson, Mahaffey, & Sutton, 1988). In a very early study Ruchkin et al. (1988) have shown that slow potentials during arithmetic tasks became more negative with increasing task demands. In accord with that finding, Rösler et al. (1997) argued that the amplitude size of slow cortical potentials represent the resources which are allocated to a task. It has further be shown that slow potentials during retention vary with the number of task-relevant objects (Arend & Zimmer, 2011; Lehnert & Zimmer, 2008; Mecklinger & Pfeifer, 1996; Ruchkin & Canoune, 1995). Bosch, Mecklinger and Friederici (2001) demonstrated that slow potentials became more positive when object information has to be stored compared to spatial information. García-Larrea and Cézanne-Bert (1998) considered such potentials as "suitable to study the 'executive' functions governing attentional and working-memory control" (p. 268). These findings suggest that slow potentials in general reflect cognitive activity during maintenance of visual information. In some cases the pure memory load modulated slow waves whereas others interpreted conceptual load to be the generator of slow wave differences during retention of visual information.

A special case of slow potentials is illustrated by the contralateral delay activity (CDA). The CDA is calculated as a difference wave using half-field versions of the CDT by subtracting the ipsilateral brain activity from the contralateral one at posterior-parietal sites (Vogel & Machizawa, 2004). By doing so, task-related unspecific bilateral brain activity such as effort related to performing the task in general, is removed whereas only storage induced activity remains (Vogel & Machizawa, 2004). The resulting difference wave therefore was interpreted to reflect the number of stored objects and reaches its asymptote when the individuals capacity maximum is achieved (Fukuda, Awh, & Vogel, 2010; Ikkai, McCollough, & Vogel, 2010; McCollough et al., 2007; Vogel & Machizawa, 2004). This component is sometimes also called sustained posterior contralateral negativity (Jolicoeur, Brisson, & Robitaille, 2008; Robitaille & Jolicoeur, 2006). Although the CDA was interpreted to reflect only set size, item complexity seems to modulate CDA as well (Gao et al., 2009; Woodman & Vogel, 2008). Woodman and Vogel (2008) could show that CDA amplitude increased for all set sizes when a more complex feature (orientation) was task-relevant compared to the easy feature condition (color). Further it could be shown that the CDA reaches its asymptote earlier when more complex objects were used (Gao et al., 2009; Gao, Ding, Yang, Liang, & Shui, 2013).

Although the CDA was introduced as ERP component reflecting the pure number of stored objects, it is to some degree ambiguous what it actually reflects. In half-field CDT participants are usually instructed to fixate on the screen center while the study array appears on the left or right side. Accordingly, the crucial visual information is presented beyond the foveal vision. When stimuli are more complex, presentation of objects in the para foveal visual field can cost some resolution and therefore prevent objects from successfully entering the VWM. By using a central version of CDT we assume that stimuli are presented in the center of the visual field and VWM capacity is not vitiated by extra foveal processing.

1.2 Storage Capacity

An intensely discussed topic is the question of how many objects can be stored in VWM. Initially seven items were thought to be maintained in working memory with an interindividual variation of plus or minus two (Miller, 1956). Further research stated that rather four objects can be hold in working memory (Cowan, 2001). This fairly fits with current findings that suggest that on average three to four simple objects can be stored in VWM (Luck & Vogel, 1997).

But how can we estimate the maximum number of stored items for an individual person? One way is to focus on performance. When two items are presented in a CDT and after a sufficient number of trials accuracy is close to 100%, we can assume that this person is able to store 2 objects. However, when four items are presented and accuracy is about 75%, is the maximum capacity of this person three? To estimate the individual capacity maximum Pashler (1988) developed an index by using corrected recognition rates and current set size. This index can be calculated using the formula K = PR*N, where K is the estimated capacity, PR refers to corrected recognition rates (p(hits) – p(false alarms)) according to Snodgrass and Corwin (1988), and N is the set size. When a person reaches a PR-score of .84 when four items are presented the K-index can be calculated as K = .84*4. It can thus be assumed that the given person can store 3.36 objects in VWM. However, VWM capacity is not only influenced by set size, but is also highly dependent on the number of task-relevant features or complexity of objects. This matter will be discussed in the subsequent chapter.

1.2.1 Object Complexity

It has been observed that not only the number but also the type of feature to be maintained in VWM is a capacity limiting factor (Eng et al., 2005). Alvarez and Cavanagh (2004) showed that capacity varies from 1.6 items when shaded cubes to about 4.4 items when colored squares were presented in a CDT. Likewise, VWM capacity for random polygons as relevant feature was found to be lower than for a feature as color (Song & Jiang, 2006) or basic shapes (Gao et al., 2009). A part of this effect may be caused by a more demanding comparison process between the test item and the memory representation if features are complex (Awh, Barton, & Vogel, 2007; Scolari, Vogel, & Awh, 2008), but other results demonstrate that also storage demands vary with stimulus complexity. E.g. Gao et al. (2009, 2013) showed that the CDA during maintenance is influenced by the type of to-be-memorized feature. Further it has been demonstrated that the CDA amplitude increased when a more demanding feature like orientation was task-relevant compared to color (Woodman & Vogel, 2008). Similarly, Luria, Sessa, Gotler, Jolicoeur and Dell'Acqua (2010) reported that the CDA was higher for visually complex than for simple items and it was argued that neurons have to "work harder" to store more complex objects. Hence, it can be concluded that complexity of to-be-memorized objects influences capacity and CDA, respectively.

1.3 Object Representation

Since capacity of VWM is highly limited, a central question is how objects are represented (for an overview see Luck & Vogel, 2013). Most of the theories can be assigned to object-based or feature-based models which will be explained in the following chapters.

1.3.1 Object-based Models

According to the object-based view, VWM capacity is confined purely by the number of objects whereas it is unimportant which or how many features are represented (Fukuda, Awh, & Vogel, 2010; Luck & Vogel, 1997; Vogel et al., 2001; Xu, 2002). For instance Luck and Vogel (1997) demonstrated that performance in change detection was the same when participants had to focus on one (e.g., color) compared to four different features (gap, size, orientation, color) of the presented objects. This effect was also observed when two features per object of the same dimension where task-relevant (e.g. two colors) (Luck & Vogel, 1997; Vogel et al., 2001). Even when a capacity exceeding number of objects was presented it was shown that participants store a small number of objects with representations containing many details instead of storing many objects with low resolution (Zhang & Luck, 2008). Further evidence for the object-based position is provided by the contralateral delay activity (CDA), an electrophysiological negativity which can be observed contralateral to the visual hemi-field in which the to-be-memorized items appear. The amplitude of the CDA increases with the number of memorized items and reaches its asymptote at the individual's maximal memory performance. The CDA is therefore considered as an estimate of the number of stored items (Vogel & Machizawa, 2004). In support of the object-based view, it was shown that the CDA amplitude is a function of the number of maintained items not of the features until the individual capacity limit is achieved (Luria & Vogel, 2011; McCollough et al., 2007; Vogel & Machizawa, 2004; Wilson, Adamo, Barense, & Ferber, 2012). Proponents of the object-based view postulate that the capacity limit is set by the individual number of "slots" available for storing integrated objects rather than individual features separately, suggesting that the number of features defining an object does not influence capacity.

1.3.2 Feature-based Models

In contrast to the object-based and in accordance with a feature-based position, other researchers reported that the amount of information held in VWM does not only depend on the number of perceived objects but also on the number of their features (Bays & Husain, 2008; Bays, Wu, & Husain, 2011; Oberauer & Eichenberger, 2013; Olson & Jiang, 2002). A corollary hereof is that it is task dependent which features are stored and that features may differ in their storage demands. Two types of results were stressed in support of this position: memory declines with an increasing number of to be maintained features and it declines if the critical features are perceptually more demanding, e.g. shapes of random polygons versus colors. Oberauer and Eichenberger (2013) found that performance decreased strongly when more features per object were relevant. Bays and Husain (2008) observed that locations of items were remembered less precisely with increasing set size. Wheeler and Treisman (2002) suggested that storage in VWM is feature specific with limited resources within dimensions, e.g., two colors versus one color, and no competition for resources between dimensions, e.g., color and orientation. This model is based on the finding that performance on conjunction of features from different dimensions is on the same level as in the single feature condition (Wheeler & Treisman, 2002). Strong conjunction costs were observed if features belonged to the same dimension (e.g., color-color-conjunctions) (Delvenne, Cleeremans, & Laloyaux, 2010; Olson & Jiang, 2002). Costs of conjunctions were not always reported, though (Luck & Vogel, 1997; Luria & Vogel, 2011). Interestingly, also inconsistent results were reported using the CDA. When different features (e.g., orientation or color) of the same objects were critical, the CDA varied with the type of feature even though the number of objects was constant (Gao et al., 2013; Luria et al., 2010; Woodman & Vogel, 2008). This demonstrates that the CDA is not unambiguously an indicator of the number of objects and may also reflect other aspects of processing. The majority of results, however, support the assumption that memory load is influenced by the number and quality of an object's features and not only by the number of presented objects itself.

1.4 Effort in Visual Working Memory

As discussed in the previous chapter ERPs during maintenance of visual information in some cases reflect feature specific differences (Gao et al., 2013; Luria et al., 2010; Woodman & Vogel, 2008). This indicates that even when the same number of objects is stored independently of the number and kind of relevant features, the *effort* to store these items may be different. The object-based view might be right in the assumption that the number of objects sets a limit to memory capacity but nevertheless the effort invested per item may vary with the quality of features. This option is supported by results from brain imaging studies. For example, it has been shown that activity in the parietal cortex – a core region of the VWM network – increases with the number of to be memorized items (Xu & Chun, 2006; Xu, 2007). This increase of neural activity was less pronounced when the items were trained and therefore more easily memorized (Zimmer, Popp, Reith, & Krick, 2012) which suggests that brain activity of the VWM network during CDT reflects the amount of processing demands. Alike, Song and Jiang (2006) showed that performance was lower and neural activity was higher when the items' shape (a complex polygon) was relevant than when only its' color was relevant. Interestingly, in a condition where both color *and* shape were task-relevant, brain activity and performance was on the level of the shape-only condition (Song & Jiang, 2006). The same result was observed in a behavioral study by Brockmole, Parra, Della Sala, and Logie (2008). This contradicts the object-based view and suggests that color is an easy feature which seems to be remembered together with demanding features like random polygons without additional costs. In a study by Sala and Courtney (2007), making color task-relevant was even facilitative: in the color-shape-conjunction condition the same memory performance was reached with less neural activity compared to the shape-only condition (Sala & Courtney, 2007).

The review of studies on VWM in this chapter demonstrates that findings in respect of factors defining load of VWM are highly controversial. Some studies are more compatible with an object-based view, whereas others demonstrate that also processing demands of task-relevant features influence memory load. It was often argued that the CDA is a pure and preferable measure of memory because processing effects are removed from the data by subtracting ipsilateral from contralateral potentials. However, by doing so also task-relevant differences in processing effort are cancelled out (cf. Vogel & Machizawa, 2004). The difference wave may therefore be a good measure for the number of objects that can be attended in WM but does not give insights into how this memory is provided. Brady, Konkle and Alvarez (2011) suggested an alternative model of how objects are represented in VWM. According to this model item representations are hierarchical with objects on the top and structural descriptions of object features on lower levels (see Figure 1-1). Creating a new object representation is therefore associated with general “overhead costs” whereas adding features to an existing object representation benefits from its existing structure (Brady et al., 2011). With this model of representation it is possible observing effects of the number of objects even though the underlying networks representing the objects’ features differ in complexity.

In order to disclose complexity related effects in VWM during maintenance a further online measure is necessary that is not only sensitive to the number of objects but also to demands of the memory tasks. One issue addressed in this dissertation project is to scrutinize effects of effort evoked by the task demands. For that purpose we decided to use the measure of pupillometry that was proven as a useful indicator of mental effort in contexts such as working memory or attention tasks.

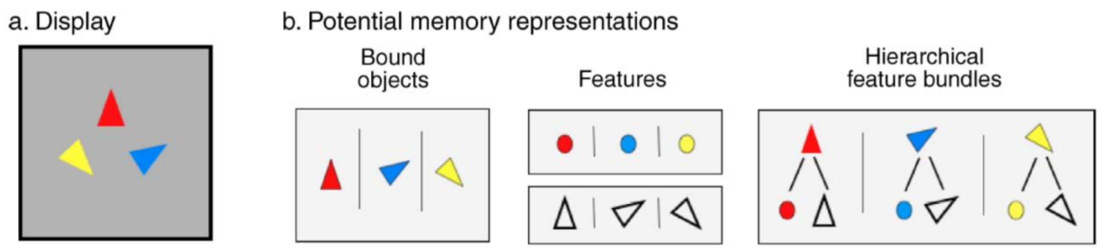

Figure 1-1. Illustration of object-representation in VWM. (A) Possible study display. (B) Schematic illustration of possible memory representation within the object-based model, the feature-based model, and with hierarchical feature bundles. Taken from Brady, Konkle & Alvarez (2011).

2 Pupillometry as Measure of Cognitive Evoked Processes

Mental effort can be sub-divided in general and task-specific mental effort and the amount of mental effort that can be exerted is limited (Kahneman, 1973). As a measure of invested mental effort, Kahneman (1973) introduced pupil measures suggesting that "the pupil at any time during performance reflects the subject's momentary involvement in the task" (p. 19).

2.1 Pupil Size and Processing Effort

The role of the pupil size during cognitive tasks was investigated in many studies (for review see Beatty, 1982; and Beatty & Lucero-Wagoner, 2000). Dilations of the pupil were observed when participants solved digit span tasks (Kahneman & Beatty, 1966; Klingner, Tversky, & Hanrahan, 2011; Peavler, 1974). The common finding of these span studies is that pupils dilate during presentation of stimuli as a function of set size until the retention phase and decrease during recall of the memorized digits. Other researchers found the pupil dilation to follow increases of difficulty in arithmetic tasks (Ahern & Beatty, 1979; Hess & Polt, 1964): in these studies, two numbers were presented sequentially with the instruction to multiply both and during the multiplication phase pupil size increased as a function of processing load. In language processing tasks increasing pupil sizes were also observed in more difficult conditions (Hyönä, Tommola, & Alaja, 1995; Just & Carpenter, 1993; Wright & Kahneman, 1971). Dilations of the pupil as a function of task difficulty were shown as well in a visual search task (Porter, Troscianko, & Gilchrist, 2007) as well as a consequence of incongruent trials in a Stroop task (Laeng, Ørbo, Holmlund, & Miozzo, 2011).

In general, we can conclude that a dilation of pupil is observed when a task becomes more difficult. Above mentioned findings and interpretations discussing pupil sizes to reflect memory load are mainly based on results from span tasks. However, executive control and rehearsal processes are also necessary to perform such tasks and could therefore as well elicit pupil changes. Hence, results on span tasks lack on defined information on what the pupil response really reflects. If pupils really reflect pure memory load, can we use it within change detection tasks?

2.2 Pupil Size and Attention

A very early finding by Beatty (1982) already confirmed attention to impact the pupil response. Two sounds of different frequencies were sequentially presented in a random order. Participants were instructed to focus only on one of the sounds indicating its detection by key-press. An increasing pupil diameter following the sound occurred only for the relevant one suggesting that the orientation of attention can affect pupil dilation (Beatty, 1982). More recent evidence for pupils involved in attentional processing was provided by Geva, Ziva, Warsha, and Olchik (2013). The authors conducted an attention network task and observed enlarged pupil diameter in cued compared to uncued trials which was interpreted to reflect an alerting state (Geva et al., 2013). Similarly, in a multiple object tracking task Alnæs et al. (2014) explained increasing pupil size when more objects are task-relevant by enhanced attentional effort. Pupil as well can indicate attentional shifts e.g. in necker-cube tasks (Einhäuser, Stout, Koch, & Carter, 2008). In this study participants had to indicate via key-press when a perceptual switch happened while looking at a 3-dimensional cube. Every time when participants indicated a perceptual switch a pupil dilation was observed (Einhäuser et al., 2008) which can be explained with attentional direction towards the "new" percept. In the next chapter the neural underpinnings of cognitive evoked pupil responses will be discussed.

2.3 Basis of Cognitive Evoked Pupil Response

2.3.1 The Role of the Locus Coeruleus

In contrast to light related changes that can increase pupils by 120%, cognitive driven changes are much smaller and recent research has outlined a relationship between pupil changes and the locus coeruleus (LC) (for review see Laeng, Sirois, & Gredebäck, 2012). The LC is a small structure within the brainstem responsible for production of norepinephrine (NE). The LC responds to stress by increasing NE production and it is involved during emotional memory retrieval (Sterpenich et al., 2006). Further it has been demonstrated that LC activity in rats increased during slow-wave sleep after a learning session (Eschenko & Sara, 2008) leading to the conclusion that the LC is involved in memory consolidation processes. Looking closer at the attentional network it was elaborated that an optimal arousal within the LC is necessary to perform well on attention tasks (Howells, Stein, & Russell, 2012). Most important in the current context is the finding that changes in pupil sizes depend on varying activity within the LC (Aston-Jones & Cohen, 2005; Murphy, O'Connell, O'Sullivan, Robertson, & Balsters, 2014). Pupil diameter and corresponding LC activity during a signal detection task with monkeys is illustrated in Figure 2-1 (Aston-Jones & Cohen, 2005). This finding could be confirmed by Alnæs et al. (2014) who could predict activity in the LC from pupil changes elicited by attentional effort in a multiple object tracking task. Earlier findings already provided evidence that activity in the LC depends on task difficulty in visual discrimination tasks (Rajkowski, Majczynski, Clayton, & Aston-Jones, 2004) and signal detection tasks (Usher, Cohen, Servan-Schreiber, Rajkowski, & Aston-jones, 1999) in monkeys. The LC-NE system is further associated with attentional processes (Aston-Jones, Rajkowski, & Cohen, 1999) which will be further discussed in the subsequent chapter.

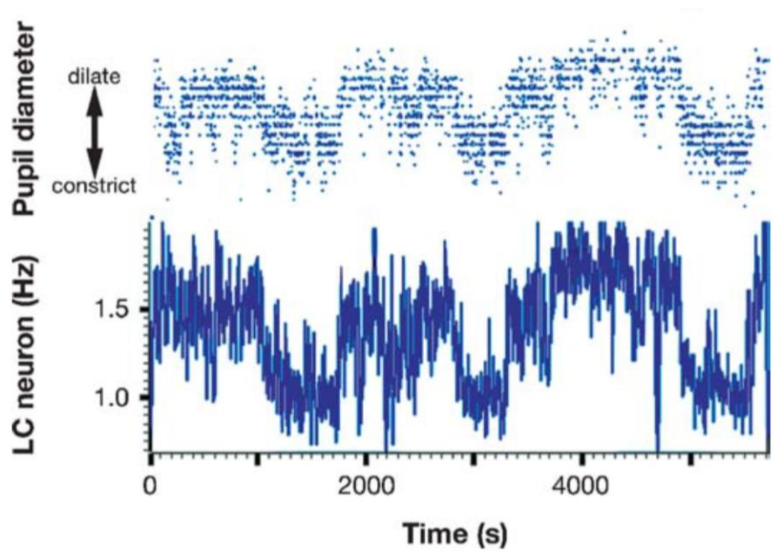

Figure 2-1. Relationship between pupil changes and LC activity. Pupil signal (top) and LC activity (bottom) during a signal detection task in monkeys. Taken from Aston-Jones & Cohen (2005).

2.3.1 Tonic and Phasic Activation

Two types of activity were found within the LC (Aston-Jones & Cohen, 2005). The tonic activity takes place in the frequency range of 2-3 Hz and is associated with poor performance on a specific task (Nieuwenhuis, Aston-Jones, & Cohen, 2005). When tonic LC activity increases, distractibility through novel stimuli is high which can be seen as an advantage during exploration. It was demonstrated that high levels of tonic LC activity correspond to high perceived mental effort (Howells, Stein, & Russell, 2010). In contrast during phasic activation the LC oscillates with about 20 Hz and this usually precedes response selection processes (Nieuwenhuis et al., 2005). Phasic activations are therefore associated with high performance on a specific task (Aston-Jones & Cohen, 2005) and are rather associated with internal categorization processes than with the pure presentation of stimuli (Nieuwenhuis et al., 2005). Further, two modes of attention where ascribed to tonic and phasic activity of the LC and the pupil size respectively (McClure, Gilzenrat, & Cohen, 2006; Nieuwenhuis et al., 2005). In the exploitation mode the phasic activity of the LC is high producing high performance on a specific task. The exploitation mode refers to "continue what you are doing" (Aston-Jones & Cohen, 2005; Usher et al., 1999) allowing high performance within the current task. In the exploration mode the tonic LC activity increases leading to a high level of general cognitive ability (Aston-Jones & Cohen, 2005; McClure et al., 2006). Within exploration mode it is suggested to "disengage and choose between one of the alternative possibilities" (Aston-Jones & Cohen, 2005; Einhäuser et al., 2008; Usher et al., 1999).

Pupillary effects reported in Chapter 2.1 and 2.2 presumably refer to the exploitation mode of attention and therefore reflect phasic activity. All studies required focused attention on a specific task such as span tasks (Kahneman & Beatty, 1966; Klingner et al., 2011), multiple object tracking (Alnæs et al., 2014) or arithmetic tasks (Ahern & Beatty, 1979; Hess & Polt, 1964). In the Experiment 1-3 we therefore also expect to find pupil changes which reflect the exploitation mode since focused attention is necessary to solve the CDT task.

3 Summary

Taken together capacity of VWM is determined by the number of objects, their complexity, and in some cases by the number of task-relevant features. An open question concerns mental effort that we have to exert to store a given set of objects. Does mental effort vary purely with the number of task-relevant objects or does the nature of task-relevant features impact mental effort? In Section 2 we therefore aimed to disentangle the constructs of capacity and task-related effort using slow waves and pupillometry during maintenance of visual information in CDT. In Experiment 1 we converged on the idea to use pupil measures in a CDT and combined this measure with ERP slow waves in Experiment 2. Experiment 3 was conducted to further investigate the role of pupil response in maintenance of visual information by constructing a cued version of the CDT. Experiment 4 served as a control study to prove that our observed pupil effects were exclusively caused by task demands and not by pure luminance characteristics of the used stimuli.

Section 2
Costs of Maintenance in Visual Working Memory

4 Experiment 1: Costs of storing color and complex shape in visual working memory: insights from pupil size and slow waves (1)

4.1 Introduction

Capitalizing on the findings reported in Chapter 2 we used pupil diameter to estimate the cognitive effort which is necessary to provide a specific memory performance. Participants worked on a change detection task for different sets of objects and features and we simultaneously measured pupil size. We expected to obtain complexity and set size effects in the behavioral data as was shown in earlier studies (Song & Jiang, 2006; Wheeler & Treisman, 2002). Additionally, we expected to see changes in pupil size as a correlate of the invested cognitive effort. It was hypothesized that, in spite of identical visual input, VWM performance and cognitive effort varies with processing demands of the critical features.

Identical items were always presented (colored polygons) but participants were required to solve different memory tasks. In different blocks either color, shape or both features were task-relevant which refers to the factor task-condition. According to the object-based view, items should be processed holistically, and therefore, task-condition should neither influence storage in VWM nor the effort that is necessary to reach a specific performance level. In contrast, if the type of feature is relevant for memory capacity, performance for color should be higher than for shape, and the latter should cause more cognitive effort leading to and increased pupil dilation. In order to additionally manipulate memory demands, we varied set size across three levels (1, 2, 4 objects) which also should influence performance and pupil diameter. At the performance level, we expected better performance in the color than in the shape condition, whereas the both condition should be at the level of shape condition (Brockmole et al., 2008; Song & Jiang, 2006). In general, a decreasing performance should be visible with increasing number of task-relevant objects. Regarding pupil sizes as measure of cognitive effort a dilation of the pupil with increasing demands is expected as found in earlier studies (Beatty, 1982; Kahneman & Beatty, 1966; Klingner et al., 2011). Pupil size should increase with the number of objects and it should correspond to the difficulty of the task-relevant features.

4.2 Methods

4.2.1 Participants

Twenty-three undergraduates from Saarland University were tested and received eight euro per hour or course credits for participation. Due to too many misses in eye tracking data two participants were excluded, so that the final sample consisted of 21 participants (10 female) with a mean age of 23.6 (19-28) years. All participants had a normal or corrected-to-normal vision and were right handed. Furthermore all participants gave their informed consent.

4.2.2 Stimuli

As stimuli, seven random polygons (see Figure 4-1) were constructed and each was generated in seven different colors resulting in a total of 49 stimuli. When presented each polygon subtended 1.4° in its longest axis. The colors were red (RGB: 255, 0, 9), green (60, 255, 0), yellow (255, 255, 0), purple (195, 0, 255), blue (0, 111, 255), cyan (0, 255, 238) and dark gray (207, 207, 207). Since dark gray was used as stimulus color all polygons were placed on a white quadratic patch of the same size as the item to make shapes better distinguishable from background which was light gray (206, 200, 200). In the study display objects could appear on four possible positions around the midpoint of the screen. Positions were corners of a virtual square whose midpoint was pseudorandomly rotated around the center of the screen. The mean distance of an object to the center of the screen was 4.8° visual angle (3.1°-6.4°) and the width and height of the virtual square was 7°. A subset of all possible positions was pseudorandomly sampled so that for each set size each position was used equally often. The combinations of objects and colors on the different positions were counterbalanced.

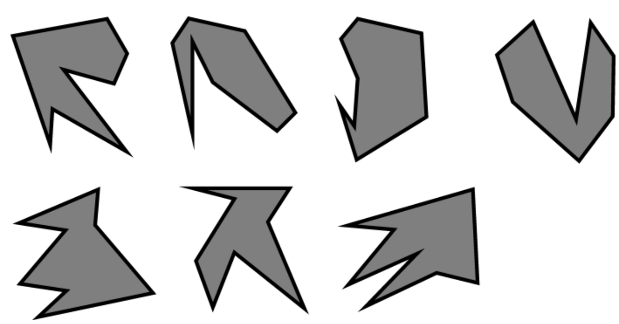

Figure 4-1. Polygons used in Experiments 1-5. For exact RGB values of the colors see Chapter 4.2.2.

4.2.3 Procedure

For stimulus presentation and data recording, E-Prime 2.0 (Psychology Software Tools, Inc.) was used. Participants underwent a visual change detection task whose trial procedure is illustrated in Figure 4-2. Each trial started with a fixation-cross which was randomly presented for 200-400 ms followed by a 200 ms blank screen. Then the study display appeared for 500 ms consisting of one, two or four objects. Objects were randomly sampled from the stimulus set, with the constraint, that neither a shape nor a color was repeated. Thereafter an empty retention interval of 1500 ms followed. During the subsequent test display only one object was shown at the same location as during the study display and participants had to indicate on a Cedrus Response Pad (RB-834, Cedrus Corporation) whether the object was the same as in the study display or had changed. The time for the test display was self-paced with a maximum of 2500 ms. A 2000 ms inter stimulus interval preceded the next trial.

Three task-conditions were realized in blocked mode. (1) In the color condition, participants were instructed that only color of the presented objects could change from study to test. (2) In the shape condition only shape could change and (3) in the both condition participants were instructed that either color or shape could have changed in the test display but never both. In case of a change always a color or shape was selected that was not used in the preceding study display. The order of these blocked task-conditions was counterbalanced across participants. In each task-condition 240 trials were presented. Additionally, set size was manipulated in random order within task-conditions. Half of the trials were change trials which led to an amount 40 change trials and 40 no-change trials per task-condition and set size. In total participants performed 720 trials. Every 40 trials participants were given a chance to make a short break. The whole session lasted about 90 minutes.

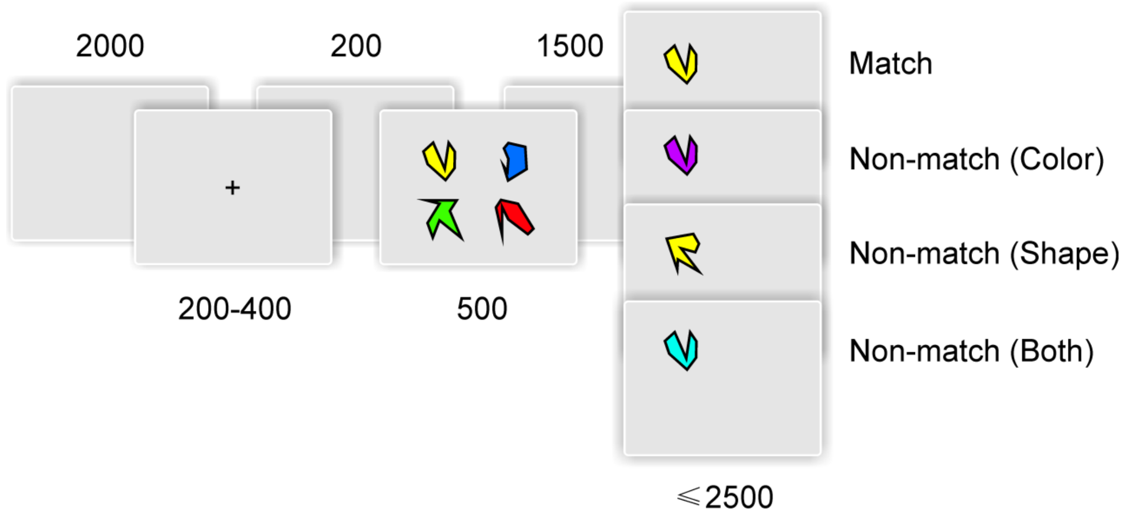

Figure 4-2. Schematic illustration of the trial structure in Experiment 1 and 2. Note that in Experiment 1 all polygons were additionally placed on a white square to make them better distinguishable from the background. Time designation in milliseconds.

4.2.4 Eye Tracking Apparatus

For measuring pupil sizes a Tobii TX300 remote eye tracker (Tobii Technologies, 2011) was utilized. The device consists of a 23 inches computer LCD monitor with a resolution of 1920 x 1080 pixels and the eye tracking unit which is placed below the monitor. The sampling rate of the machine is 300 Hz with binocular eye tracking. The TX300 can compensate for head movements up to 50 cm/sec. However, we instructed participants to move as little as possible. The eye tracker was placed on a table in a dimly lit room and participants were placed with a distance of 65 cm in front of the monitor in a comfortable chair.

4.2.5 Preprocessing of Pupil Data

To avoid losing too many data the signal was linearly interpolated when pupil was lost for less than 500 ms. (e.g., due to blinks). Then, a trial based segmentation was conducted using a baseline of 200 ms prior to the onset of the study display. The time window of interest was defined as subset of the retention interval in accordance to former studies (Beatty, 1982; Kahneman & Beatty, 1966; Klingner, Kumar, & Hanrahan, 2008). From previous research it is known that the pupil response for cognitive driven changes is delayed by 100-200 ms (Beatty, 1982). Hence, pupil data were analyzed in the interval between 700 and 2200 ms after onset of the study display. Mean average pupil sizes of the time window of interest were computed and the signals of left and right pupils were averaged.

4.2.6 Statistical Analyses

For performance data as well as for pupil data repeated measurement ANOVAs were conducted. When sphericity was violated the p-level was adjusted according to Greenhouse and Geisser (1959) and the uncorrected degrees of freedom were reported. Post hoc tests were conducted by alpha adjusted paired-samples t-tests.

4.3 Results

4.3.1 Behavioral Results

For analyses of performance corrected recognition rates (PR) (Snodgrass & Corwin, 1988) were calculated as proportion of hits minus proportion of false alarms for each set size and task-condition. PR-scores and K-indices are illustrated in Figure 4-3. Statistical analyses were conducted for PR-scores only since K-indices are linear transformations of PR-values. They are illustrated to provide information about estimated capacity within the different conditions and were calculated as PR*set size (as described in Chapter 1.2).

A 3 × 3 repeated measurement ANOVA with factors Task-condition (color, shape, both) x Set size (1, 2, 4) revealed significant main effects of set size, $F(2, 40) = 281.4$, $MSE = 2.87$, $p < .001$, $\eta_p^2 = .93$, and task-condition, $F(2, 40) = 68.5$, $MSE = .46$, $p < .001$, $\eta_p^2 = .77$, and a significant interaction of these two factors, $F(4, 80) = 28.77$, $MSE = .12$, $p < .001$, $\eta_p^2 = .59$

(see Figure 4-3). As visible in Figure 4-3, in the shape or both condition highly similar performances were observed. In contrast if only color was task-relevant memory performance decreased less with increasing set size. This difference between color condition and shape or both condition induced the obtained interaction effect. To statistically show this pattern we analyzed shape and both condition in a separate 2 (shape, both) × 3 (1, 2, 4) ANOVA. As expected the interaction was no longer significant, $F(2, 40) = .58$, $MSE = .002$, $\eta_p^2 = .03$. The main effect of set size remained, $F(2, 40) = 330.44$, $MSE = 2.79$, $p < .001$, $\eta_p^2 = .94$, and the main effect of task-condition was small, $F(1, 20) = 3.98$, $MSE = .03$, $p = .06$, $\eta_p^2 = .17$. Memory performance in the color condition was better than in the shape and both condition at all levels of set size even if performance was close to the ceiling as in set size 1, $t(20) = 3.28$, $p < .01$, and indeed in set sizes 2 and 4, $t(20) = 5.7$, and $t(20) = 11.91$, $p < .001$, respectively.

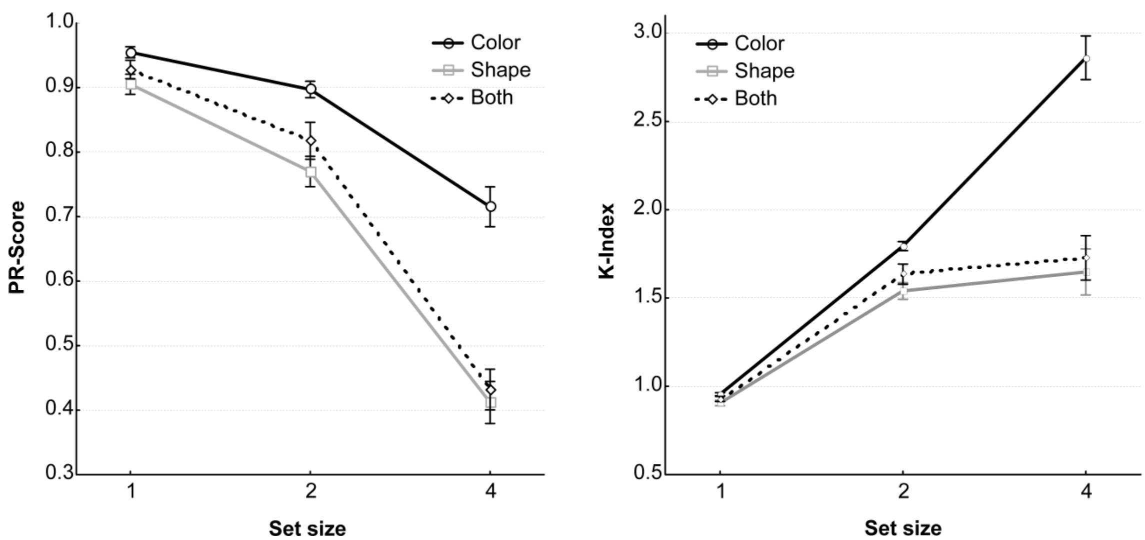

Figure 4-3. PR-Scores and K-indices of all conditions and set sizes from Experiment 1. Bars reflect standard errors.

4.3.2 Pupil Data

For statistical analyses of pupil data we averaged pupil diameter in the time window of 700-2200 ms after the onset of study display. The averages are reported in Table 4-1 and the time course of pupil dilation can be seen in Figure 4-4.

A 3 × 3 repeated measurement ANOVA with factors Task-condition (color, shape, both) and Set size (1, 2, 4) revealed a significant main effect of set size, $F(2, 40) = 23.38$, $MSE = 18.22$, $p < .001$, $\eta_p^2 = .54$, but not for task-condition, $F(2, 40) = .82$, $MSE = .11$, $\eta_p^2 = .04$, and a significant interaction, $F(4, 80) = 4.17$, $MSE = .5$, $p < 01$, $\eta_p^2 = .17$. In order to reveal the origin of this interaction we analyzed set size effects separately for each task-condition. Set sizes differed always significantly, $F(2, 40) = 14.23$, $MSE = 6.36$, $p < .001$, $\eta_p^2 = .42$, $F(2, 40) = 26.58$, $MSE = 6.7$, $p < .001$, $\eta_p^2 = .57$, and $F(2, 40) = 19.16$, $MSE = 6.17$, $p < .001$, $\eta_p^2 = .49$, for color, shape and both condition, respectively. However, in the color condition the difference between set size 1 and 2 was small and only marginally significant $t(20) = -1.94$, $p = .07$. The pairwise differences between all other set sizes in color, shape and both condition were clearly significant (smallest t-value, t = 2.11). Additionally, we tested task-condition effects at different levels of set size. Significant differences were obtained only for set size 2, $F(2, 40) = 8.42$, $MSE = .99$, $p < .001$, $\eta_p^2 = .3$, set size 1 and 4 did not show effects of task-condition, $F(2, 40) < 1$. At set size 2, shape showed increased pupil size compared to the color condition, $t(20) = 2.48$, $p < .01$, but only a marginal significant difference in pupil size was observed between bot condition and the shape condition, $t(20) = -2.00$, $p = .06$. Taken together, pupil data reveal a general increase of pupil size with set size in all conditions but only when two objects were presented, the task-condition seemed to play a role (color < shape ≤ both).

Table 4-1

Mean changes of pupil size during retention compared to baseline of Experiment 1 and 2. Changes are indicated in millimeter.

	Condition	Set size 1	Set size 2	Set size 4
	Color	-.042 (.01)	-.012 (.02)	.052 (.02)
Experiment 1	Shape	-.048 (.01)	.001 (.02)	.051 (.02)
	Both	-.048 (.01)	.022 (.02)	.042 (.02)
	Color	-.051 (.01)	-.038 (.02)	.024 (.01)
Experiment 2	Shape	-.072 (.02)	-.047 (.02)	.011 (.01)
	Both	-.060 (.01)	-.045 (.01)	.001 (.01)

Standard deviations are reported in parentheses.

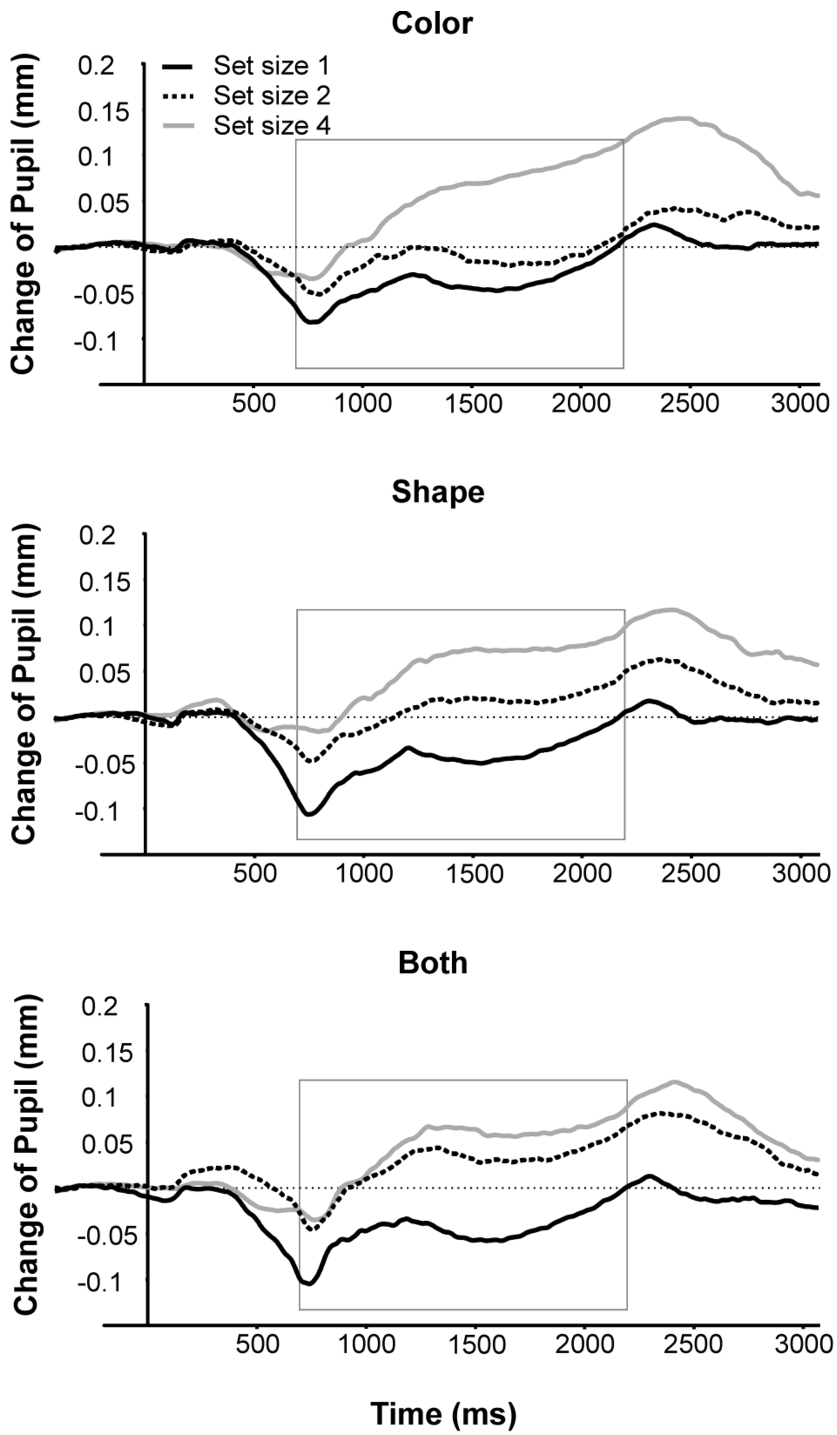

Figure 4-4. Time course of changes of pupil size in Experiment 1. Pupil sizes are illustrated relative to baseline for color condition (top), shape condition (middle), and both condition (bottom). Time window of analyses (700-2200 ms after onset of study display) is marked by the gray fringe.

4.4 Discussion

The behavioral data clearly showed that VWM is influenced not only by the number of objects but also by the type of task-relevant feature. Maintaining more objects in VWM led to a decrease in performance which was much more pronounced when shape was task-relevant. Shape changes were generally detected more poorly than color changes. When shapes became relevant, as in the shape and both condition, performance dropped compared to maintaining colors. However, if in addition to shape, color had to be memorized performance was not worse than if only shape was relevant. This replicates the results of Song and Jiang (2006). Two explanations for this result are at hand: (1) it is possible that the easy feature color can be added to the complex feature shape without costs, or (2) that color and shape are always represented as bound features if shapes are voluntarily maintained. For example, to represent the complex shape of a random polygon, focal attention is probably necessary and this may automatically integrate shape and color (Treisman & Gelade, 1980).

Dilations of the pupil were observed with ascending number of objects in all task-conditions. Between task-conditions only differences of pupil size were found when participants had to process two objects. It is obvious that pupils' diameter, observed during the retention interval, followed the number of maintained objects. This finding is consistent with previous work where participants had to remember digits in span tasks (Beatty, 1982; Klingner et al., 2011) and it is consistent with the assumption that cognitive effort increases with set size. However, we did not observe the expected increase with task difficulty across task-conditions. We found such differences only for set size 2 and even there they were not very strong making possible that it is an accidental effect. At set size 4 which exhibited the largest effect of task-condition on performance, we did not obtain any task-condition effect in pupil diameter. Either pupil dilation is not sensitive for this variation in cognitive effort or the differences in performance between task-conditions are not caused by differences during storage in VWM. The first alternative is possible if pupil diameter is only sensitive to the number of objects to that attention is directed but not to processing effort. For example, it can be a correlate of the degree of alerting caused by the number of displayed objects. The second alternative could mean that maintenance effort does not vary with task-conditions, and the differences in performance originated in the comparison process during the test display (Awh et al., 2007). This latter interpretation would strongly support the assumption that mental effort in VWM is defined purely by the number of objects. To decide between these two interpretations a second experiment was conducted. In Experiment 2 we aimed to replicate the pupil data to make sure that they are reliable. In addition, we collected electrophysiological data to additionally measure cognitive effort.

5 Experiment 2: Costs of storing color and complex shape in visual working memory: Insights from pupil size and slow waves (2)

5.1 Introduction

The goal of the second experiment was to replicate the behavioral and pupillary findings of Experiment 1. The same visual change detection paradigm as in Experiment 1 was used but additionally brain potentials were recorded as a further online measure to estimate mental effort while the different features were maintained in VWM.

As already discussed the contralateral delay activity is not applicable because by the way of its calculation effects of processing demands are removed from the data (cf. Vogel & Machizawa, 2004). Slow potentials on which the CDA is based seem to be more suitable. Their amplitudes should get larger with increasing processing effort. Rösler, Heil and Röder (1997) argued that the amplitudes of slow cortical potentials correspond to the resources which are allocated to a task. Accordingly, Mecklinger and Pfeiffer (1996) could demonstrate, that maintaining different numbers of objects leads to differences in slow potentials. Similarly, Lehnert and Zimmer (2008) observed that slow potentials varied with the number of objects in VWM. Finally, in some studies, slow potentials fitted behavioral data even better than the CDA (e.g. Arend & Zimmer, 2011). Therefore slow cortical potentials were measured during maintenance and their mean amplitudes were used as dependent variable.

Since the same design was realized, a replication of the behavioral and pupil data of the first experiment was expected. One interpretation of the pupillary findings from the first experiment was that pupil diameter indicates the number of processed objects. The pupillary response would then be a correlate of attentional effort which is higher when more objects are to attend. If this is correct, similar effects in an early electrophysiological correlate of attention should be visible. Between 125 and 175 ms after stimulus onset, a negative component (N1) is often observed which is typically considered as attention related component that is associated with orienting attention to task-relevant stimuli (Luck, Heinze, Mangun, & Hillyard, 1990). According to this view, the pupillary response and the N1 amplitude should show similar effects.

The second prediction concerns slow waves in the retention interval. Set size and task-condition related performance differences were expected which should come along with differences in cognitive effort. Therefore slow waves should show condition differences if maintenance effort varies not only with the number of items but also with task-condition.

5.2 Methods

5.2.1 Participants

Twenty-three undergraduates underwent the experimental procedure. Five participants were excluded due to eye tracking or EEG artefacts. The final sample consisted of 18 (11 female) participants with a mean age of 23.65 (19-31) years. All participants were right handed and had normal or corrected-to-normal vision. All participants received eight euro per hour and gave their informed consent.

5.2.2 Stimuli

The same polygons as in Experiment 1 were used in the visual change detection task but they were presented with slight modifications. The color dark gray (RGB: 207, 207, 207) was replaced by orange (244, 122, 0) because this color can be more easily discriminated from the background and the shapes could therefore be directly presented on the gray background without the white square behind. This should make sure that the varying number of objects did not influence luminance. Even this is unlikely given the late onset and the long duration of the pupil signal in Experiment 1. To ensure that pupil response in the current study is only elicited by cognitive processes, luminance of all stimuli and of the background was measured. We used a LUNASIX F (Gossen-Metrawatt, Nürnberg) light meter and measured luminances directly on the display using a fibre optic. The following values were obtained (all in candela/m^2): red 52.5, purple 70, blue 64.17, cyan 127.92, green 105, yellow 150.42, and orange 58.33. The average luminance of these stimuli is 89.76 cd/m^2, which is roughly the same as the luminance of the background (93.33 cd/m^2). Additionally, compared to the background, the area of the stimuli was small, why we do not assume that the presented objects caused significant differences in total luminance. In addition we conducted a control study to rule out effects of luminance in our pupil results which is described in Chapter 7.

5.2.3 Procedure

The procedure was the same as in Experiment 1. Also the same eye tracking apparatus was used and preprocessing of pupil data was done in the same way as in the first experiment. Including preparation for EEG recording the whole session lasted between 2 and 2.5 hours.

5.2.4 Electrophysiological Recording

The EEG was recorded from 32 active electrodes of an Acticap-system (Brain Products, Munich) which were mounted in an elastic cap. An electrode on the right mastoid was used as online reference and data were re-referenced offline to electrodes on the left and right mastoids. Ground electrode was placed at AFz position. As positions of the electrodes a subset of the international 10-20 system (Fp1, Fp2, F7, F3, Fz, F4, F8, C3, Cz, C4, P3, Pz, P4, O1, O2) was used with additional positions mainly at posterior and parietal sites (FC6, FC5, T7, T8, P8, P7, PO7, PO9, PO3, POz, Oz, PO4, PO8, PO10). Horizontal and vertical eye movements were recorded monocular with electrodes below and on the temple of the right eye. All impedances were kept below 10 kilo-ohms. During data recording the active shield function of the Acticap-system to suppress noise from the surrounding was activated. Data were recorded with a sampling rate of 1000 Hz and an online filter with a high-cutoff value of 250 Hz. Because we were interested in slow potentials no online low-cutoff filter was used to avoid distortions within the frequency of interest.

5.2.5 Preprocessing of EEG Data

For data preprocessing, Vision Analyzer 2.0 (Brain Products, Munich) was used. Corrections of eye movements were done according to the method described by Gratton, Coles and Donchin (1983). Further, a high-cutoff filter of 30 Hz was conducted offline to eliminate high frequency noise in the signal. A baseline of 200 ms prior to the onset of the study display was created leading to a length of 2400 ms for each data segment. Since a centralized version of the change detection task was used, no lateralized effects were expected. A Hemisphere × Task-condition × Set size ANOVA revealed no significant main effect or interaction with the factor hemisphere ($p > .14$) Therefore a bilateral posterior cluster was created for statistical analyses (PO3, PO7, PO9, PO4, PO8, PO10, O1, O2).

To analyze the N1, peak to peak amplitudes between P1 and N1 were calculated. For P1 peak detection a time window of 100-180 ms was used, whereas for detection of the N1 peak amplitude the time window 120-220 ms was used.

5.3 Results

5.3.1 Behavioral Results

PR-scores and K-indices are illustrated in Figure 5-1. As in Experiment 1 statistical analyses were conducted only for PR-scores. K-indices are provided to gain coarse information concerning capacity. In a 3 × 3 repeated measurement ANOVA of the PR-scores with the factors Task-condition (color, shape, both) × Set size (1, 2, 4) we observed significant main effects of set size, $F(2, 34) = 181.53$, $MSE = 2.07$, $p < .001$, $\eta_p^2 = .91$, and task-condition, $F(2, 34) = 40.31$, $MSE = .36$, $p < .001$, $\eta_p^2 = .7$, and again a significant interaction of both factors, $F(4, 68) = 13.4$, $MSE = .09$, $p < .001$, $\eta_p^2 = .46$ (see Figure 5-1). As in Experiment 1, performance in the shape and both condition showed a highly similar pattern. In a separate 2 × 3 repeated measurement ANOVA with factors Task-condition (shape, both) and Set size (1, 2, 4), only the main effect of set size was significant, $F(2, 34) = 156.68$, $MSE = 2$, $p < .001$, $\eta_p^2 = .9$, but not the interaction, $F(2, 34) = .34$, $\eta_p^2 = .02$. The main effect of task-condition reached only a marginally level of significance, $F(1, 17) = 3.23$, $MSE = .02$, $p = .09$, $\eta_p^2 = .16$. Thus performance in the shape and both condition was similar and differed from the color condition as in the Experiment 1.

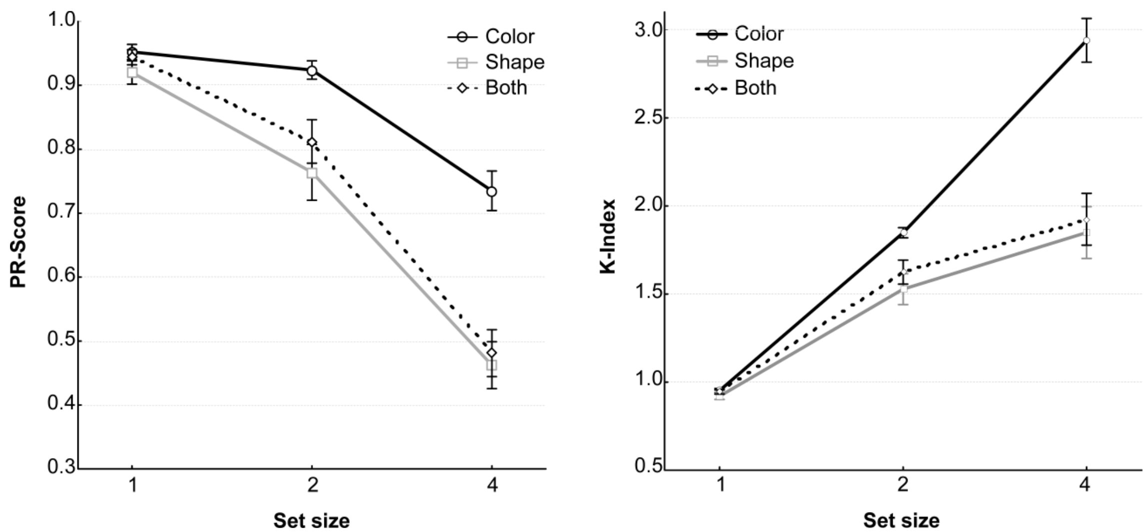

Figure 5-1. PR-Scores and K-indices of all conditions and set sizes from Experiment 2. Bars reflect standard errors.

5.3.2 Pupil Data

A 3 (color, shape, both) × 3 (1, 2, 4) repeated measurement ANOVA with mean pupil sizes in the time window 700-2200 ms after onset of the study display showed a significant main effect of set size, $F(2, 34) = 24.41$, $MSE = .00$, $p < .001$, $\eta_p^2 = .59$, but neither of task-condition, $F(2, 34) = 1.53$, $\eta_p^2 = .08$, nor a significant interaction of both factors, $F(4, 68) = 1.09$, $\eta_p^2 = .06$. Pupil diameter was larger in set size 2 than in 1, $t(17) = 3.07$, $p < .01$, and in set size 4 compared to 2, $t(17) = 4.75$, $p < .001$. Pupillary time courses of different task-conditions and set sizes are depicted in Figure 5-2, and mean averages are reported in Table 4-1.

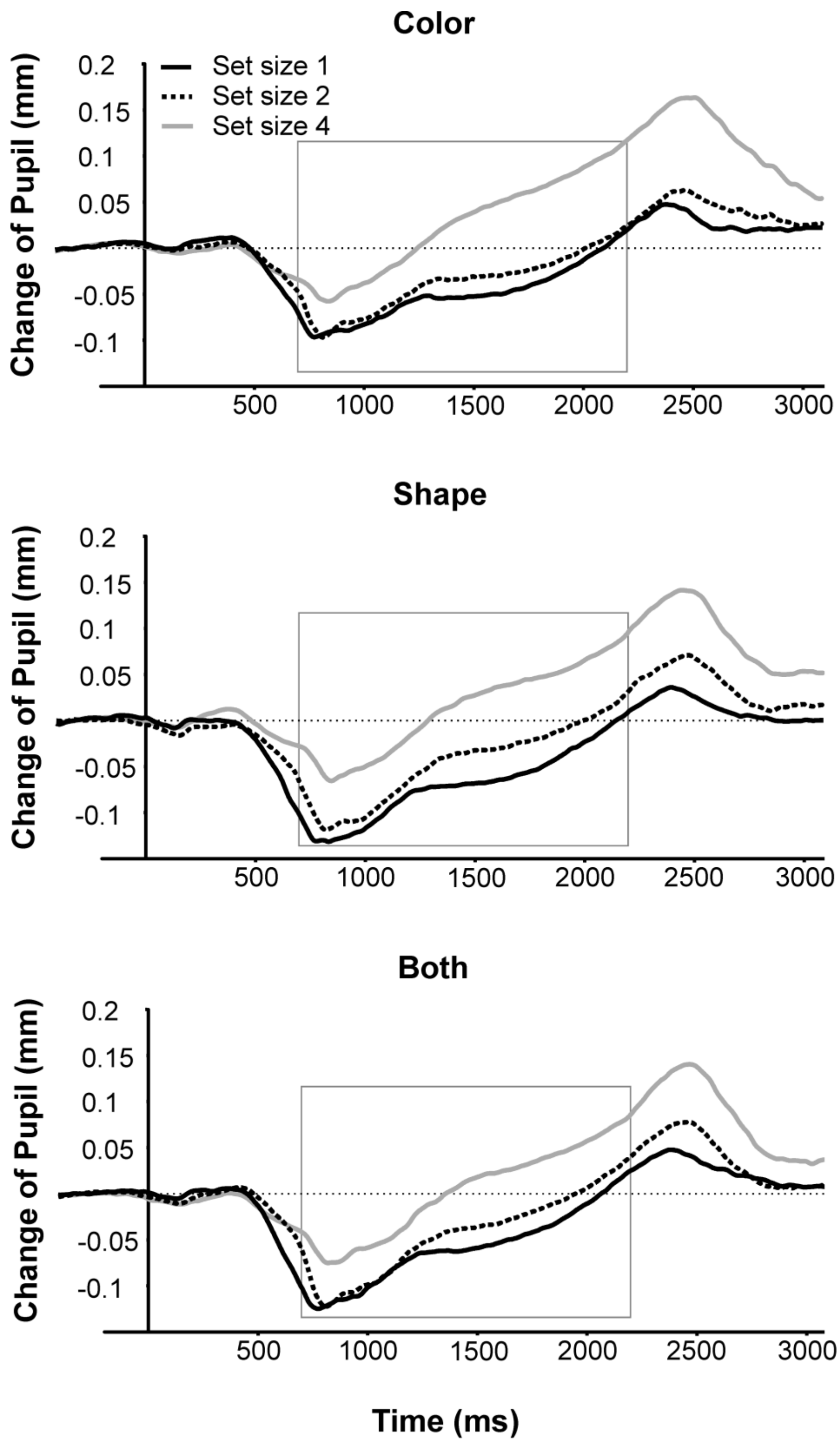

Figure 5-2. Time course of changes of pupil size in Experiment 2. Pupil sizes are illustrated relative to baseline for color condition (top), shape condition (middle), and both condition (bottom). Time window of analyses (700-2200 ms after onset of study display) is marked by the gray fringe.

5.3.3 Electrophysiological Data

5.3.3.1 Time Window 120-220 ms (N1)

A repeated measurement ANOVA with the factors Task-condition × Set size for the size of the N1 amplitude revealed a significant main effect of set size, $F(2, 34) = 21.86$, $MSE = 273.6$, $p < .001$, $\eta_p^2 = .56$ but no further effects (see Figure 5-3). Both pairwise differences between set sizes were significant, $t(17) > 2.39$, $p < .05$. Therefore N1 amplitude solely increased with set size but no task-condition dependent variation was observed. Since we had additionally speculated that the N1 component and pupil diameter may reflect similar processes, the values of both variables were z-standardized and analyzed in a combined repeated measurement ANOVA with factors Type of measure (N1, pupil size) × Task-condition (color, shape, both) × Set size (1, 2, 4). A significant main effect of set size was obtained, $F(2, 34) = 42.92$, $MSE = 30.81$, $p < .001$, $\eta_p^2 = .72$, but no other effect $F(2, 34) < 1.35$. This result is evidence that the common factor which elicits changes in both measures is only set size.

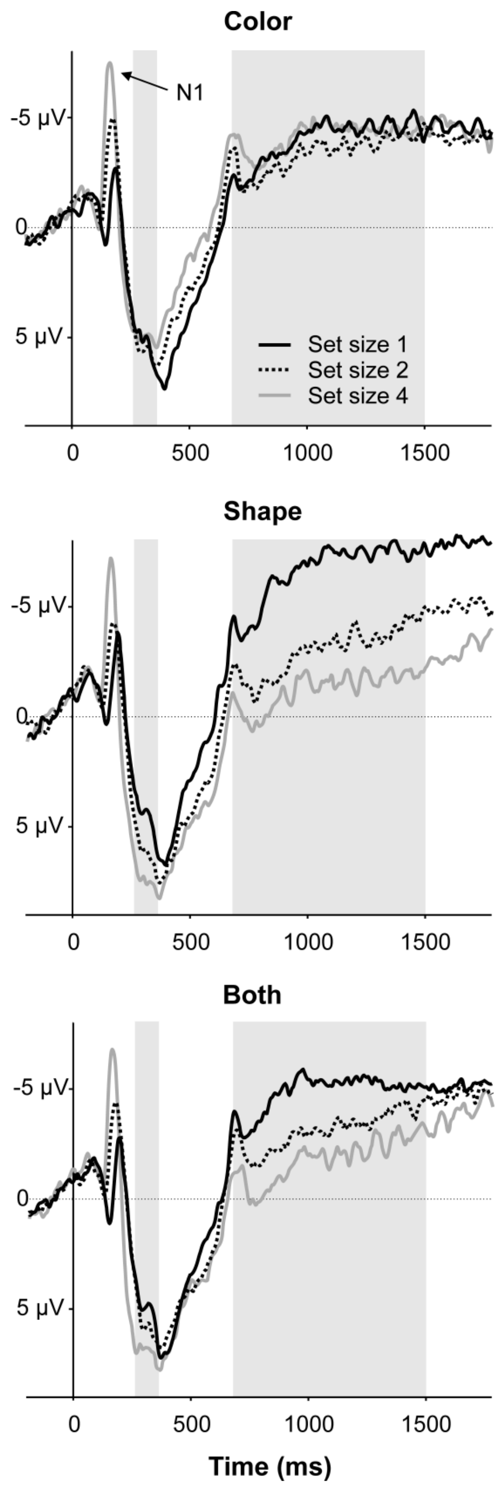

Figure 5-3. Grand average ERPs from Experiment 2. ERPs at posterior cluster (see chapter 5.2.5) for color condition (top), shape condition (middle), and both condition (bottom). N1 was calculated via peak detection and is marked by a black arrow (top); P2 (270-370 ms) and slow wave (700-1500 ms) time windows are marked by gray areas.

5.3.3.2 Time Window 270-370 ms (P2)

By visual inspection of the event related potentials another effect was evident which is modulated by task-condition in the time window of 270-370 ms. In order to test this, mean amplitudes were calculated as an estimator of the size of this component (see Table 5-1). A Task-condition × Set size ANOVA on these amplitudes revealed a significant interaction of both factors, $F(4, 68) = 5.04$, $MSE = 12.14$, $p < .05$, $\eta_p^2 = .23$. In the color condition different effects compared to the shape and both condition were observed. No P2 modulation by set size was visible if color was relevant, $F(2, 34) = .55$, $\eta_p^2 = .03$. In a separate 2 (shape, both) × 3 (1, 2, 4) ANOVA of the other two task-conditions in which shape was one relevant feature a clear effect of set size was observed, $F(2, 34) = 6.57$, $MSE = 6.39$, $p < .01$, $\eta_p^2 = .28$, but no other effects (all p > .18). Amplitudes went more positive with increasing set sizes. The results show that shape and both condition revealed the same set size dependent positive going waveforms whereas no set size effect was found in the color condition.

5.3.3.3 Time Window 700-1500 ms (slow potentials)

For the time window 700-1500 ms after onset of study display mean amplitudes of the bilateral posterior cluster were computed. A Task-condition × Set size repeated measurement ANOVA revealed a significant main effect of set size, $F(2, 34) = 18.58$, $MSE = 113.68$, $p < .001$, $\eta_p^2 = .52$, but not of task-condition, $F(2, 34) = 1.17$, $\eta_p^2 = .06$. A significant interaction of set size and task-condition, $F(4, 68) = 7.31$, $MSE = 36.11$, $p < .01$, $\eta_p^2 = .30$, was additionally found (see Figure 5-3). Color strongly differed from shape and both condition which were rather similar. We therefore separately analyzed these task-conditions as we had done for performances and P2 amplitudes. For the color condition, no differences between set sizes were observed, $F(2, 34) = .61$, $\eta_p^2 = .03$. In a separate 2 (shape, both) × 3 (1, 2, 4) ANOVA, a clear set size effect was found, $F(2, 34) =25.7$, $MSE = 6.56$, $p < .001$, $\eta_p^2 = .6$, but no main effect of task-condition, $F(1, 17) = 1.21$, $\eta_p^2 = .07$, and a weak interaction, $F(2, 34) = 3.2$, $MSE = 4.47$, $p = .05$, $\eta_p^2 = .16$. All pairwise comparisons of mean amplitudes between set sizes were significant (minimum $t(17) = 2.96$, $p < .01$), except of the difference between size 2 and 4 in the both condition, $t(17) = 1.74$, $p = .10$. As Figure 5-3 shows, the interaction effect origins from a somewhat smaller set size effect in the both condition compared to the shape condition. For set size 1, the amplitude was larger in the shape than in the both condition, $t(17) = 2.66$, $p < .05$. A separate 2 × 2 analysis of the other two set sizes did only show a significant main effect of set size, $F(1, 17) = 12.93$, $MSE = 3.22$, $p < .01$, $\eta_p^2 = .43$, but no main effect of task-condition or interaction (all $p > .55$). As found within the P2 amplitudes, slow waves during retention were similar during shape and both condition and differed from the color condition.

Table 5-1

Mean amplitudes of P2 and slow waves of Experiment 2.

	Condition	Set size 1	Set size 2	Set size 4
P2	Color	5.48 (.92)	5.70 (.98)	5.06 (.72)
	Shape	4.86 (.92)	6.43 (.96)	7.61 (.90)
	Both	5.58 (.93)	6.15 (1.21)	7.15 (.99)
Slow waves	Color	-4.04 (.62)	-3.40 (.54)	-4.16 (.80)
	Shape	-6.73 (.74)	-3.02 (.64)	-1.27 (.75)
	Both	-4.86 (.45)	-3.07 (.69)	-1.78 (.85)

Standard deviations are reported in parentheses.

5.4 Discussion

Performance and pupil data of Experiment 2 replicate those of Experiment 1. Additionally, slow brain potentials provided further insights into the storage mechanisms of the different task-conditions. Electrophysiological data showed clear set size differences for shape and both condition, and both were rather similar as it has already been observed for the performance data. This effect was not found when the easy color was task-relevant. Furthermore, during the N1 time window a set size dependency within all conditions was observed which corresponded to the pupil data.

The behavioral findings suggest reliably that the performance limit was determined by the more complex feature - in this case the shape of the random polygons - and color did not add anything to memory load. Probably it was always encoded if an object was attended during shape encoding. The pattern of changes in pupil size from Experiment 1 was also replicated. Dilation of the pupils was observed with increasing set size but no effects of task-condition were found. It is therefore assumed that pupil sizes in this working memory task reflect attentional effort initiated by the number of objects to be encoded into memory. This is supported by the observation that also the N1, which is assumed to indicate orientation of attention to targets, showed a similar pattern as the pupil data.

In contrast slow waves during the retention interval showed effects of task-condition. They exhibited more positive going waveforms with increasing set size in the shape and both but not in the color condition. Such slow potentials should correspond to the invested cognitive effort (Rösler et al., 1997) which suggests that in shape and both condition additional cognitive processes were engaged that are absent in the color condition. That these two task-conditions differ was also suggested by the differences in the P2 component. When shape was relevant, set size effects were observed which were absent in the color condition. Working memory tasks that need shape information seem to be processed differently than tasks that solely need color information. It is speculative what kind of cognitive process generated these potentials, but the strong set size dependent slow waves in the shape and both condition suggest that participants continued actively processing the set of items during retention. In contrast, the potentials in the color condition look alike keeping the representation of colors as created at the end of encoding. Clearly, the kind of task-relevant feature did not only influence accuracy at the moment of test. It triggered different processes during maintenance of the items.

6 Experiment 3: Mental effort in the time course of change detection as revealed by event-related pupil response

6.1 Introduction

In Experiment 3 we aimed to focus on task-related effort during the maintenance phase of visual information provided by pupil measures. In addition we investigated task engagement more extensively by allowing participants to prepare for the number of task-relevant objects. Therefore we developed an extended cueing version of a change detection task where random polygons were presented within a color and a shape condition. Initially a cue informed participants about the number of presented objects. During the following cue-target interval (CTI) participants could prepare for the study display which had to be maintained in VWM until the test display. If the set size dependent mental effort is driven by a general task engagement we hypothesized that (1) the cued number of objects should influence pupil during the CTI already and (2) set size should impact pupil during retention. Phasic pupil changes in this task are expected to correspond to the exploitation mode (see Chapter 2.3.1) since task-specific high performance is necessary.

6.2 Methods

6.2.1 Participants

The experiment was conducted at the Institute of Psychology within in the Chinese Academy of Sciences in Beijing. A total of 37 participants were tested each receiving 50 Yuan for the 90 minutes testing session. Five participants had to be excluded from the final sample (four because of low eye tracking quality, one because of a computer malfunction). The final sample consisted of 32 undergraduate participants (23 females) with a mean age of 23.09 years (SD = 2.15). All participants had a normal or corrected-to-normal vision and gave their informed consent.

6.2.2 Stimuli and Procedure

As stimuli the same seven random polygons each in seven different colors were utilized as in Experiment 1 and 2, which were presented on a gray background (206, 200, 200). Stimuli were displayed on a virtual pentagon rotating around the center of the screen. The radius of the pentagon was 3.59° visual angle and the size of a polygon was 1.4° visual angle. Dependent on set size a subset of the five possible positions was sampled.

The trial structure is illustrated in Figure 6-1. At the beginning of each trial the number of task-relevant objects was cued in the center of the screen for 500 ms followed by a 2000 ms cue-target interval (CTI). Then the study display appeared for 500 ms. After a 1500 ms retention interval only one object was presented during the self-paced test display up to 2500 ms. A 1500 ms ITI preceded the next trial. Two task-conditions and 5 set sizes were included. Participants were instructed that either the color or the shape is task-relevant during the following block and that only the task-relevant feature could change. The task then was to indicate via pressing the keys “z” or “m” on a computer keyboard that the presented object had changed compared to the corresponding object in the study display or not. The assignment of keys to response category was counterbalanced across participants. A block consisted of 50 trials and task-condition changed after every block. Short breaks were included between blocks accompanied by the instruction to close eyes for a rest. Set sizes 1, 2, 3, 4 and 5 were randomly mixed within the blocks. A total of 500 trials were performed leading to an amount of 50 trials per set size and condition. Before participants started the experiment they performed 15 color and 15 shape trials in a practice block.

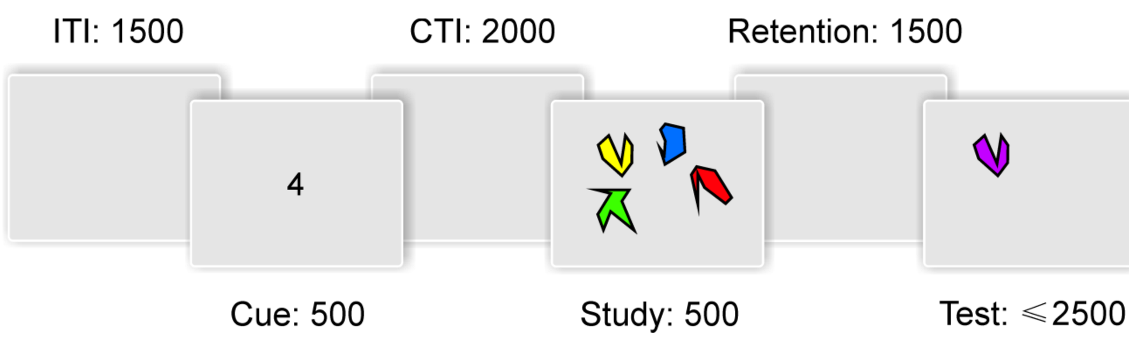

Figure 6-1. Trial structure of Experiment 3. The example illustrates a non-match trial within the color condition. Time designation in milliseconds.

6.2.3 Preprocessing of Pupil Data

To record the pupils signal a Tobii T60XL remote eye tracker with a sampling rate of 60 Hz and a 24 inches monitor with a resolution of 1920 x 1200 pixels was used. Participants were placed 65 cm in front of the monitor in a dimly lit room. To improve data quality and to avoid head movements a chin rest was used. For analyses, signals of both eyes were averaged and missing data with a length up to 400 ms were linearly interpolated. The signal then was segmented with a baseline 200 ms prior to the onset of the cue with a length of 5200 ms. Hence it is possible to calculate statistics during different epochs of the trial. Pupil sizes during the CTI were calculated using the time window of 700-2500 ms after onset of the cue whereas pupil sizes during retention where calculated between 3200 and 4500 ms after onset of the cue. According to Beatty (1982) a latency of 200 ms was assumed to precede cognitive evoked pupil responses.

6.3 Results

6.3.1 Behavioral Results

PR-scores and K-indices are illustrated in Figure 6-2. As in the previous experiments, statistics were only conducted for PR-scores. A 2 × 5 repeated measure ANOVA with factors Task-condition (color, shape) and Set size (1, 2, 3, 4, 5) revealed significant main effects of task-condition, $F(1, 31) = 69.17$, $MSE = .02$, $p < .001$, $\eta_p^2 = .69$, and set size, $F(4, 124) = 189.75$, $MSE = .01$, $p < .001$, $\eta_p^2 = .86$, as well as a significant interaction of both factors, $F(4, 124) = 26.99$, $MSE = .00$, $p < .001$, $\eta_p^2 = .47$. Comparisons between color and shape performance for set size 1 and 2 showed no significant differences (all p > .63), but on the levels of set sizes 3, 4 and 5 performance in color condition was consistently better (all p < .001) compared to shape condition.

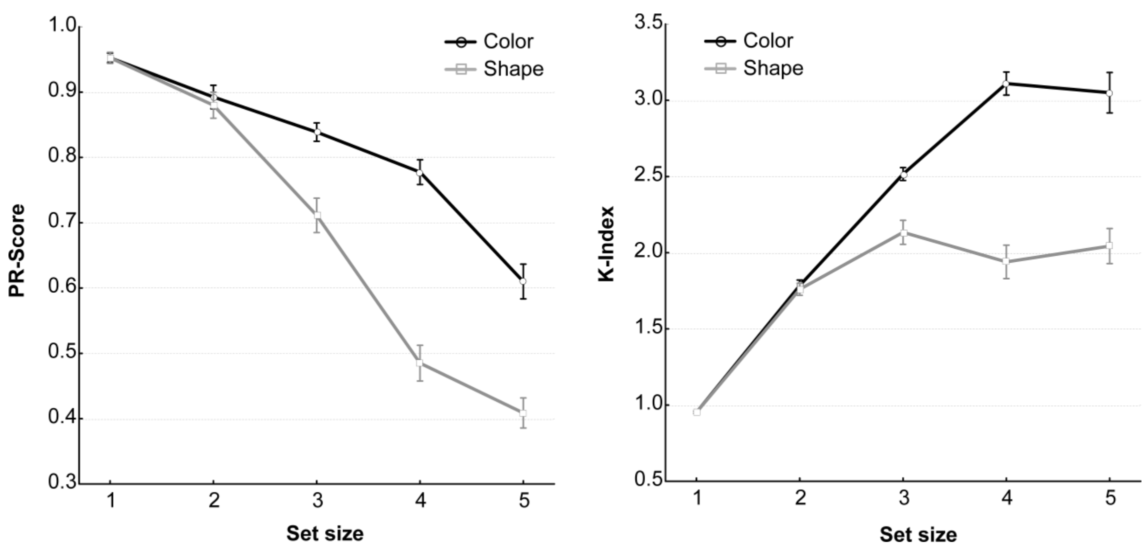

Figure 6-2. PR-Scores and K-indices of all conditions and set sizes from Experiment 3. Bars reflect standard errors.

6.3.2 Pupil Results

6.3.2.1 CTI (700-2500 ms)

For the CTI time window (700-2500 ms after cue onset) a 2 × 5 repeated measure ANOVA revealed a significant main effect of set size, $F(4, 124) = 10.51$, $MSE = .00$, $p < .001$, $\eta_p^2 = .25$, but no significant effect of task-condition or an interaction of both factors (all p > .16). As it is visible from Figure 6-3, pupil size increases with set size. Stepwise comparisons revealed a significant difference between set sizes 3 and 4, $t(31) = 2.67$, $p < .05$, but not for the other contrasts (all p > .12).

6.3.2.2 Retention (3200-4500 ms)

A 2 × 2 × 5 repeated measure ANOVA with factors Time window (early: 3200-3800 ms, late: 3800-4500 ms), Task-condition (color, shape) and Set size (1, 2, 3, 4, 5) revealed significant main effects of time window, $F(1, 31) = 58.45$, $MSE = .00$, $p < .001$, $\eta_p^2 = .65$, and set size, $F(4, 124) = 82.12$, $MSE = .00$, $p < .001$, $\eta_p^2 = .73$. Significant interactions of time window with task-condition, $F(1, 31) = 15.72$, $MSE = .00$, $p < .001$, $\eta_p^2 = .34$, and set size, $F(4, 124) = 11.36$, $MSE = .00$, $p < .001$, $\eta_p^2 = .27$, were observed. In the early time window a Task-condition × Set size ANOVA exhibited a significant main effect of set size only, $F(4, 124) = 78.50$, $MSE = .00$, $p < .001$, $\eta_p^2 = .72$. Stepwise comparisons collapsed across task-conditions between the levels of set size showed significant differences (all p < .001) except the difference between set size 4 and 5, $t(31) = 1.52$, $p = .14$. In the late time window a Task-condition × Set size ANOVA revealed significant main effects of task-condition, $F(1, 31) = 8.54$, $MSE = .00$, $p < .01$, $\eta_p^2 = .22$, and set size, $F(1, 31) = 73.35$, $MSE = .00$, $p < .001$, $\eta_p^2 = .70$. As visible in Figure 6-3, a dilation of the pupil with increasing set size as well as in the shape condition compared to color condition was observed in the late time window.

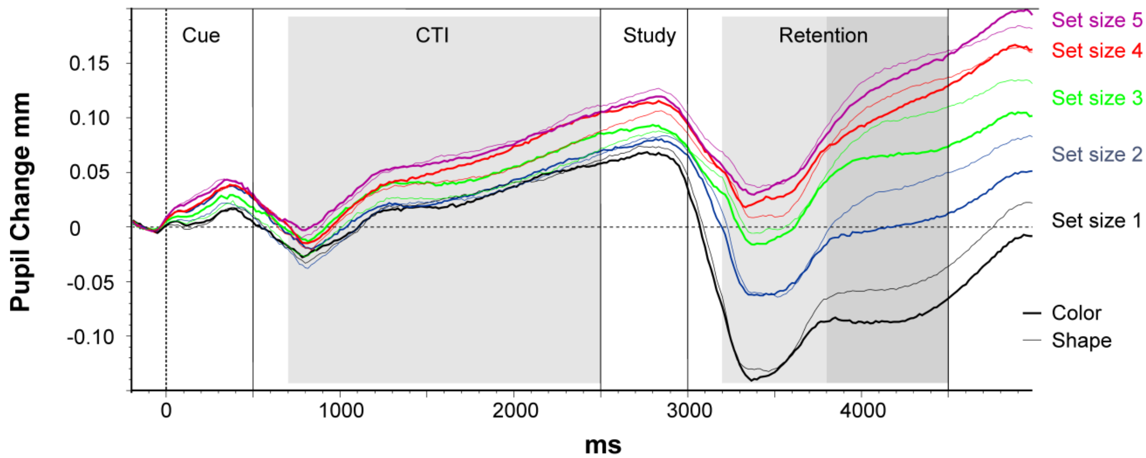

Figure 6-3. Time course of changes of pupil size in Experiment 3. Pupil sizes are illustrated relative to baseline for color condition (thick lines) and shape condition (thin lines). Time window of analyses during CTI (700-2500 ms) and during retention (early: 3200-3800 ms; late: 3800-4500 ms) are marked by gray areas.

6.4 Discussion

In Experiment 3 we aimed to demonstrate the dependency of pupil dilation on task induced effort within a change detection task. Therefore we created a CDT with a cueing phase and a retention phase. The PR-scores showed the typical pattern of a decreasing performance with an increasing number of task-relevant objects. Differences between task-conditions were observed only for set sizes 3, 4 and 5. This difference is due to the complexity difference between colors and shapes and replicates earlier findings (Song & Jiang, 2006, findings from Experiment 1 and 2). We can interpret these results as an inferior capacity of VWM for the more complex shapes compared to colors. On the level of set sizes 1 and 2 performance is the same for both conditions.

The pupil sizes during the CTI were significant larger with increasing set size. Although only the contrast between set sizes 3 and 4 was found to differ significantly an overall pattern depicting increasing pupil sizes with increasing set sizes was observed. It is clear that solely the information about the following number of task-relevant objects can elicit pupil changes. The pupil response during the CTI reflects the preparation towards the following study display and differences between set sizes are likely to depict differences in invested effort.

During the retention interval an interaction of task-condition and time window was found. A clear set size effect in the first half of the retention interval was highly significant and set sizes differed stepwise from each other except set sizes 4 and 5. In the second half additionally a task-condition effect was found. Although the visual input on the level of each set size did not differ between task-conditions a dilation of the pupil size was observed when shape was task-relevant. Interestingly the pupils dilated when shape was task-relevant compared to color condition in set sizes 1 and 2 although no differences in performance data were found. This result leads to the interpretation that mental effort in the late retention interval differed between task-conditions during maintenance even though performance is on the same level. Hence it seems that more effort is necessary in the shape condition to reach the performance level compared to the color condition. From performance data we can see the drop only when three or more items were task-relevant.

From visual working memory research it is known that capacity is highly limited which is usually accompanied by a drop in performance. However it is debated how much mental effort is necessary to solve a specific task. In Experiment 3 we could show that more mental effort is required when maintaining more complex features of objects despite the performance can be the same. This result underlines the importance of additional effort measures such as pupillometry in addition to behavioral measures.

7 Experiment 4: Control Study Luminance

7.1 Introduction

Luminance effects on the pupil were investigated in several studies (Bradley, Miccoli, Escrig, & Lang, 2008; Ellis, 1981; Kardon, 1995). As shown by Ellis (1981) the pupillary light reflex occurs 200-400 ms after light exertion and its amplitude varies from .5 up to 2.5 mm. In order to take the pupil response as evidence for task-related processes we have to exclude differences in luminance or other perceptual processes as possible reasons. We aimed directly to demonstrate the independence of the obtained pupil effects in Experiment 1-3 of such physical influences. For this reason the same colored polygons in the same arrangement as in Experiment 1 and 2 were presented but partipcants had no corresponding memory task. We expected that under these conditions the previously observed pupil signals are absent.

7.2 Methods

7.2.1 Participants

Thirtythree people participated in this experiment. Due to eye tracking artifacts two participants had to be removed from the final sample. A comparably large number of participants was tested to have enough test power because the null hypothesis was critical. With this sample size we had a test power of .8 to detect an effect of .25 size.

7.2.2 Stimuli and Procedure

The same polygons as in Experiment 2 on the same gray background and the same positions were presented. Set size (1, 2, 4 polygons) was manipulated and a zero condition was added where no polygon was present. The timing was the same as before. In order to give particpants a meaningful task we realized a CDT regarding the central fixation cross. During the study display the central object could be an “×” or “+” which should be maintained in VWM until the test display. During the test display either the same or a changed central object was presented (changes in 50 % of the time). Participants had to indicate via a key press on a Cedrus Response Pad (RB-834, Cedrus Corporation) if the central object changed. 40 trials per set size were presented.

7.3 Results

The pupil data are reported in Figure 7-1. We observed slight changes in puil size which were clearly smaller as in the previous experiments, and which sometimes were dilations and sometimes constrictions. As in Experiment 1-3, mean amplitudes during the retention interval were analyzed. A repeated measurement ANOVA with the factor Set size (0, 1, 2, 4) revealed a significant main effect, $F(3, 90) = 3.27$, $MSE = .00$, $p < .05$, $\eta_p^2 = .10$, which origins from the pupil difference between set size 2 and 4. In set size 4 the pupil was smaller (a constriction) than when two items were presented (a small dilation). This pattern of set size effects has no resemblance to the previously obtained ones and this rules out that luminance differences caused the set size dependent pupil effects in Experiment 1-3.

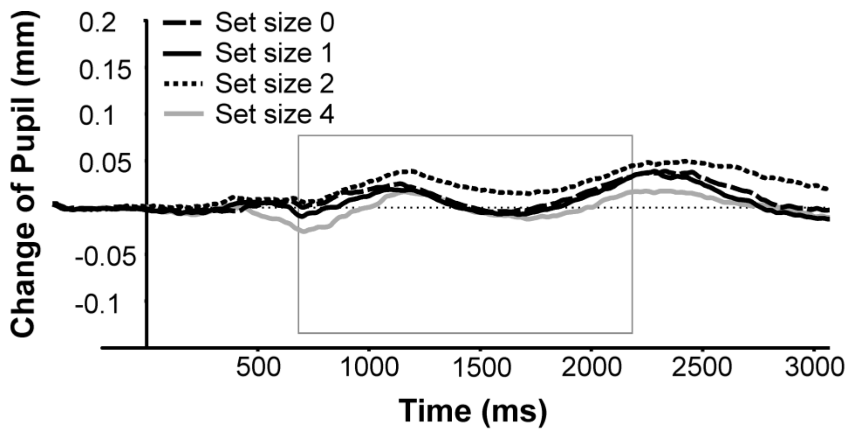

Figure 7-1. Time course of changes of pupil size in Experiment 4. Pupil sizes are illustrated relative to baseline. Time window of analyses (700-2200 ms after onset of study display) is marked by the gray fringe.

7.4 Discussion

The pupillary results of Experiment 4 indicate that differences in pupil size obtained in the previous experiments were clearly evoked by cognitive processes. The overall pattern showed no set size dependent increase of pupil diameter as in the previous studies. Nevertheless a significant main effect of set size was found which is mainly generated by the difference between set size 2 and 4 (see Figure 7-1). However when two objects were presented pupil size increased compared to set size 4. This finding is the reverse pattern compared to Experiments 1-3 where increased pupil size was observed with increasing set size.

8 General Discussion

In this section we focused on cognitive processes during maintenance of information in VWM. Pupil sizes and ERPs were used to gain information about mental costs of storage dependent on set size and feature complexity. As it could be shown in Experiment 1 and 2, pupil sizes strictly represented the number of displayed objects independent of the task-relevant feature. Therefore, we classified pupil measures in the context of a CDT as attentional effort that is necessary to focus on task-relevant stimuli. A relationship between pupil dilation and task demands was as well demonstrated by Alnæs et al. (2014) who could show that attentional effort in a multiple object tracking task correlated with increasing pupil diameter. In Experiment 3 we provided evidence that solely the information about the number of to be stored objects elicited a pupil response. This further supports our interpretation of pupil response reflecting attentional processes. When purely storing or maintenance mechanisms are the basis of the obtained pupil changes, we should not find (comparable) pupillary dilation responses in the cueing phase of Experiment 3. Since the cue consisted of one digit the perceptual visual input was always the same. Therefore at least part of the pupil effect is generated by attentional effort that is necessary to prepare for encoding of presented stimuli. In the maintenance phase of Experiment 3, a condition dependent pupil change was observed in the late time window, which was not observable in Experiments 1 and 2. Pupil size in the shape condition increased compared to the color condition as a function of feature complexity. This supports our initial hypothesis that the amount of mental effort dedicated to a task, which was supposed to be greater in the more demanding shape than color condition, should influence the pupil response. The most significant difference between the first two experiments and Experiment 3 is the manipulation of the cueing phase. In Experiment 3, participants had more time to prepare for the study display by directing their attention to the number of stimuli. In Experiment 1 and 2 the pupillary complexity effect might therefore be covered by attentional processes. In Experiment 4 we could rule out perceptual characteristics such as luminance of the used polygons to be responsible for the obtained pupillary changes.

Slow waves during retention of visual information in Experiment 2 showed a condition-dependent variation: in shape and both condition positive going slow waves were observed with increasing set size, whereas a set size effect was absent in the color condition. In line with our hypothesis, the set size differences in slow waves in the shape condition and the absence of such an effect in the color condition illustrates that storing complex shapes costs more mental effort than the storage of simple colors. Hence, it can be concluded that maintaining colors works in a more passive way whereas maintaining shapes leads to set size dependent costs in VWM.

Taken together, the results from Experiment 1-3 reported in this section lead to clear conclusions on costs of storage in VWM as depicted by pupillary and electrophysiological findings. Pupillary changes reflect costs of attentional effort associated with the number of task-relevant objects whereas slow waves represent mental effort during maintenance of the presented objects. However, what we cannot yet target is the question of how these objects are represented in VWM. As discussed in Chapter 1.3 mainly two VWM models are predominantly discussed in literature, which describe either objects and/or features as capacity limiting factors in VWM.

The aim of the last experiment of this thesis was to investigate the issue of how information is stored in VWM. For that purpose, we used behavioral and electrophysiological measures to examine ongoing processes during CDT for task-relevant and task-irrelevant information. Experiment 5 and its theoretical background will be described in the following Section 3.

Section 3
Selective Storage in Visual Working Memory

9 Selective Storage of Features

In the current section we pursue the goal of providing new insights on the topic of how objects are represented in VWM. In Chapter 1.3 object-based and feature-based models were introduced that both make assumptions about how objects are represented in VWM. The main argument coming from proponents of both models deals with decreasing or steady performance observed in CDT with multi-featured objects. It was argued that a steady performance with increasing set size - when one feature is task-relevant compared to when 4 features per object are task-relevant - provides evidence for an object-based storage whereas a decreasing performance would be in line with a feature-based view.

A further approach of investigating the nature of object representation in VWM is to focus on selective storage of features. The idea is that changes of task-irrelevant information should not influence performance when a single feature of a given object can be stored separately. To thoroughly explore this issue, ERPs can be used to gain new insights into cognitive processes following manipulation of task-irrelevant information during test. It would be evidence for the object-based VWM representation, when changes of task-irrelevant information influence performance and ERPs whereas no such influence would rather speak for a feature selective storage in VWM and thus for the feature-based model. In the following chapter findings on selective storage will be discussed.

9.1 ERP Results during Retention

As discussed in Chapter 1.3.2 differences in CDA amplitude resulting from different feature conditions were taken as evidence for feature selective encoding (Woodman & Vogel, 2008). Similarly, Luria et al. (2010) observed an increase of the sustained posterior contralateral negativity (SPCN, refers to CDA) when task-relevant features became more complex (random polygons). The SPCN increase already reached saturation at set size 2 when polygons were presented and shape was task-relevant (and therefore no further increase could be observed when four polygons were task-relevant). However in the color condition SPCN constantly increased from set size one to four. The difference between color and polygon condition was explained by harder working neurons when polygons where task-relevant (Luria et al., 2010), which in principle fits our idea of mental effort that is reflected by slow potentials during maintenance. These findings were supported by Gao et al. (2013) showing that set size related CDA differences diminished when objects became more complex.

9.2 ERP Results during Test

Above mentioned findings regarding the CDA and SPCN are clear with respect to storage of relevant information, but ambiguous in regard of storage of task-irrelevant features. To better understand this ambiguity it is necessary to consider cognitive processes depicted by ERPs during the test display where the comparison between presented and encoded information occurs. Gao et al. (2010) conducted a series of experiments in which they manipulated task-irrelevant information in CDT. They demonstrated effects of task-irrelevant information in a time window between 200 and 300 ms after onset of the test display. The authors observed a negative component around 270 ms (N270) when an irrelevant, but salient feature (e.g., color) was changed. In contrast, the N270 was absent when the feature was difficult to perceive (i.e., it was complex) (Gao et al., 2010). It was argued that salient information is extracted automatically whereas more complex information is only extracted intentionally (Gao et al., 2010). Negative components of mismatching information in this time window were also reported in the context of other tasks (see Folstein & Van Petten, 2008 for review). In general N270 reflects changes of highly discriminable information in S1-S2 tasks (Yin et al., 2011; Zhou et al., 2011). However, the absence of the N270 for task-irrelevant complex features can be a consequence of not representing these features in VWM or of not processing these features at the time of testing. In spite of this, the presence of an ERP difference elicited by changes of complex task-irrelevant features would unequivocally proof that this information was stored in VWM.

Varying task demands related to the type of task-relevant feature influences processing in VWM at the moment of memory comparison. Many studies have shown that processing capacity, mental workload and task difficulty influence amplitude and/or the latency of the P3 component (for a review see Kok, 2001). Initially, positive ERP deflections at about 300 ms after onset of task-relevant stimuli were associated with categorization and attention allocation (cf. Polich & Kok, 1995). However, a considerable body of work demonstrated latency and/or amplitude of the P3 to be sensitive to e.g. memory load (Brookhuis et al., 1981), complexity of matching operations (Ullsperger, Metz, & Gille, 1988), or to compatibility of presented stimuli (Ragot & Fiori, 1994). P3 latencies in stimulus classification tasks were found to increase with stimulus categorization difficulty (Courchesne, Hillyard, & Courchesne, 1977; Kutas, McCarthy, & Donchin, 1977). In a VWM task P3 amplitude was larger when more complex visual stimuli were task-relevant than when stimuli were simple (Liesefeld & Zimmer, 2013). It was also shown that P3 amplitude decreased with increasing memory load due to increasing set size (Brookhuis et al., 1981). However, sometimes also a temporally more extended P3 was observed which might contain different subcomponents. In a visual delayed discrimination task, Bledowski et al. (2006) isolated two P3 peaks (P366 and P586) following S2 presentation at PZ electrode. The authors interpreted the early peak as correlate of familiarity-based stimulus evaluation whereas the late peak was considered to reflect memory search operations necessary for more complex working memory tasks (Bledowski et al., 2006). From these findings it is reasonable to hypothesize that the P3 is suitable to reflect cognitive processes during comparison of VWM content and displayed stimuli. In Experiment 5 we therefore additionally focused on the P3 time window during test display.

10 Experiment 5: Correlates of information mismatch in visual working memory as a function of task-relevance

10.1 Introduction

Experiment 5 aimed to spot on the interaction of task difficulty, memory load and object representation by presenting colored objects making easy (color) or difficult features (shape) task-relevant. A CDT was conducted with varying set sizes (1, 2, 4 objects) and two task-conditions (color, shape). As shown in Experiment 2, (1) slow potentials during retention were expected to reflect task difficulty dependent on memory load driven by task-condition and set size. (2) ERP differences within the P3 time window were expected during presentation of the test display. The amplitude should be larger for non-matching than matching targets and larger for the difficult shape than for the easy color condition. Finally, (3) mismatch of task-irrelevant information should influence ERPs during test display if it is represented in memory, and this should be the case even for the difficult feature, i.e. shape.

10.2 Methods

10.2.1 Participants

Twenty-two undergraduates participated in the experiment receiving 8 Euros per hour and gave their informed consent. Due to EEG artifacts (enhanced alpha activity) one participant had to be excluded from the final sample consisting of 21 participants (16 female). All participants were right handed, had a normal or corrected-to-normal vision and reported no neurological problems. The mean age was 23.05 years (SD 4.06, range 18-31).

10.2.2 Stimuli and Procedure

Objects were presented on a 23 inches TFT screen. Seven distinctive polygons were used and each could take on seven different colors. Colors were the same as in Experiment 2 and 3 and all objects were presented on a gray background (206, 200, 200). Object positions were arranged in virtual square with a height and width of 7° visual angle rotating around the midpoint of the screen. The mean distance of an object from the screen center was 4.8° visual angle (3.1°-6.4°). Dependent on set size a subset of these positions was pseudorandomly sampled making sure that each position was equally often used across set sizes and task-conditions. Items were randomly drawn from all 49 possible shape color combinations with the restriction that neither a shape nor a color was repeated within a display.

The trial structure is illustrated in Figure 10-1. A trial always started with a central fixation cross randomly presented for 200-400 ms followed by a 200 ms blank screen. Thereafter a study display appeared for 500 ms. After the 1500 ms retention interval participants saw a test display until response but with a maximum allowed time of 2500 ms. Finally an inter stimulus interval of 2000 ms preceded the next trial. At test, only a single object was displayed at one of the study positions. Participants were instructed to compare the presented object at test with the object at the corresponding location within the study display. Responses were given by pushing one of two response buttons on a Cedrus Response Pad (RB-834, Cedrus Corporation). A Yes button should be pressed following a change and a no button when a match trial appeared. The assignment of keys to response category was counterbalanced across participants. Two task-conditions were realized: In the color condition participants were told to only focus on changes of the objects' color and to ignore shapes, whereas in the shape condition the color had to be ignored.

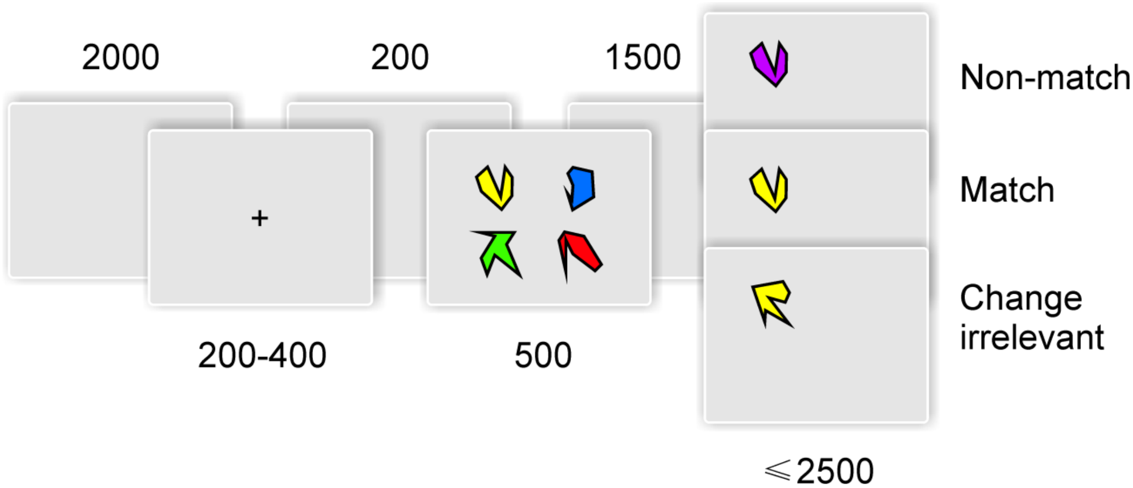

Figure 10-1. Example trial of color condition in Experiment 5. Time designation in milliseconds.

The experiment consisted of 840 trials divided into 28 blocks of 30 trials each and between the blocks short breaks were inserted. Task-condition (color, shape) was blocked, i.e. all items of a block were processed with the same instruction, but it was changed after each block. Half of the participants started with the color and half with the shape condition. The task-condition of the subsequent block was reminded during the breaks and the beginning of a block was self-paced. Three trial types were realized: A match and a non-match trial referring to the task-relevant feature and a match trial with a change of the task-irrelevant feature, in the following called match, non-match, and change irrelevant, respectively. Set size was manipulated by presenting one, two or four objects at the study display. In order to have a nearly equal number of correct trials in each cell of the design for ERP analyses, 60 trials per task-condition and trial type were presented in set size 4 whereas 40 trials per task-condition and trial type were used in set sizes 1 and 2. The whole session lasted about 120 minutes.

10.2.3 EEG Recording

EEG was recorded continuously using an Acticap-system (Brain Products, Munich) with 32 active electrodes. Ground electrode was placed at AFz position and online reference electrode was located on the left mastoid. For offline re-referencing an electrode was placed on the right mastoid. A subset of the positions according to the international 10-20 system was used (Fp1, Fp2, F7, F3, Fz, F4, F8, C3, Cz, C4, P3, Pz, P4, O1, O2). Additional electrodes were placed mainly at posterior sites (FC6, FC5, T7, T8, P8, P7, PO7, PO9, PO3, POz, Oz, PO4, PO8, PO10). Eye activity was recorded unipolar at the left canthus for vertical movements (vEOG) and below the left eye for horizontal movements (hEOG). All impedances were kept below 10 kilo-ohms. The EEG was sampled with 1000 Hz using an online low pass filter of 250 Hz and an infinite time constant.

Correction of eye blinks was conducted according to Gratton, Coles and Donchin (1983). The signal was filtered with a 30 Hz low pass filter and partitioned into 2000 ms segments for study and test display separately with a baseline of 200 ms prior to the onset of the study/test display. Only correct trials were included. For the analysis of slow waves during the retention phase on average 76 trials per task-condition were obtained for set sizes 1 and 2 and 98 trials per task-condition when four objects were task-relevant. ERPs on the target were on average based on 27 trials per task-condition and trial type in set size 1 and 2, and 33 trials in set size 4.

10.2.4 Statistical Analyses

Repeated measurement ANOVA's were conducted for behavioral and ERP analyses. Adjusted p-levels (Greenhouse & Geisser, 1959) are reported with uncorrected degrees of freedom if sphericity was violated. For post hoc analyses paired-samples t-tests were used with adjusted alpha levels.

10.3 Results

10.3.1 Behavioral Data

Accuracies decreased with increasing set size but this was modulated by task-condition and trial type (see Figure 10-2A). A repeated measurement ANOVA with the factors Task-condition (color, shape) × Set size (1, 2, 4) × Trial Type (match, non-match, change irrelevant) exhibited significant main effects of task-condition, $F(1, 20) = 58.96$, $MSE = .01$, $p < .001$, $\eta_p^2 = .75$, set size, $F(2, 40) = 143.75$, $MSE = .01$, $p < .001$, $\eta_p^2 = .88$, and trial type, $F(2, 40) = 10.00$, $MSE = .01$, $p = .001$, $\eta_p^2 = .33$, as well as a significant interaction of all three factors, $F(4, 80) = 7.74$, $MSE = .001$, $p = .06$, $\eta_p^2 = .28$. For color condition a 3 (1, 2, 4) × 3 (match, non-match, change irrelevant) ANOVA revealed a significant main effect of set size, $F(2, 40) = 52.30$, $MSE = .01$, $p < .001$, $\eta_p^2 = .72$, and a significant interaction of set size and trial type, $F(4, 80) = 3.93$, $MSE = .01$, $p < .01$, $\eta_p^2 = .16$. On the level of set size 1 and 2 no significant effects of trial type were observed (all $p > .18$) but it tended to get significant if four objects were presented, $F(2, 40) = 3.08$, $MSE = .01$, $p = .06$, $\eta_p^2 = .13$. For shape condition, a 3 × 3 ANOVA showed significant main effects of set size, $F(2, 40) = 172.52$, $MSE = .01$, $p < .001$, $\eta_p^2 = .90$, and trial type, $F(2, 40) = 20.76$, $MSE = .01$, $p < .001$, $\eta_p^2 = .51$, and a significant interaction of both factors, $F(4, 80) = 4.69$, $MSE = .01$, $p < .01$, $\eta_p^2 = .19$. For set size 1, match and change irrelevant did not differ ($p > .19$), but performance in the non-match condition was worse than in the change irrelevant condition, $t(21) = 3.08$, $p < .01$. For set size 2, performances followed the order match > change irrelevant > non-match and all pairwise differences were significant (all $p < .01$). With four objects, match and change irrelevant differed, $t(21) = 4.08$, $p < .001$, but no significant difference was found between change irrelevant and non-match ($p > .24$). To sum up, trial type did only influence performance in the shape condition. In set sizes 2 and 4, performance strongly decreased when the task-irrelevant color changed.

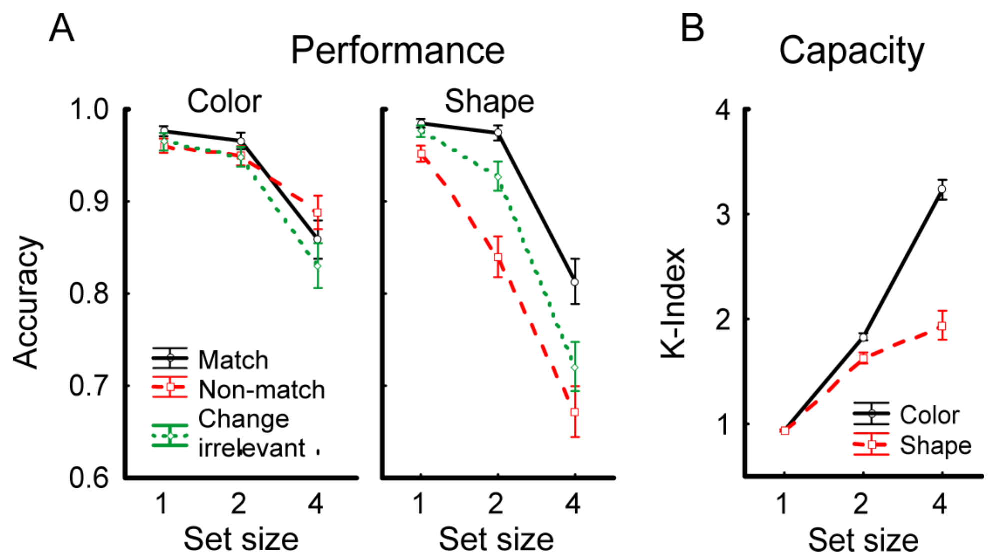

Figure 10-2. Accuracies and K-indices of Experiment 5. (A) Accuracies of color and shape condition are shown for different set sizes and trial types. (B) Capacity of color and shape condition is depicted for different set sizes. Bars indicate standard errors.

To estimate the maximum number of stored objects within the different task-conditions and set sizes K-indices were calculated as described in Chapter 1.2. K-indices for color and shape condition are depicted in Figure 10-2B. A repeated measurement ANOVA with factors Task-condition (color, shape) × Set size (1, 2, 4) revealed significant main effects of task-condition, $F(1, 20) = 105.50$, $MSE = .07$, $p < .001$, $\eta_p^2 = .84$, and set size, $F(2, 40) = 237{,}33$, $MSE = .12$, $p < .001$, $\eta_p^2 = .92$, and a significant interaction of both factors, $F(2, 40) = 105.32$, $MSE = .05$, $p < .001$, $\eta_p^2 = .84$. No difference between color and shape was observed for set size 1 ($p < .99$), but at set size 2, $t(21) = 5.22$, $p < .001$, and 4, $t(21) = 10.68$, $p < .001$, K-indices were smaller in the shape than in the color condition. Participants were able to maintain a maximum (K_{max}) of 3.2 objects when color was task-relevant while K_{max} decreased to 1.9 objects in the shape condition.

10.3.2 ERPs during Study and Maintenance

A repeated measurement ANOVA with P1 (100-180 ms) – N1 (120-220 ms) differences and factors Task-condition (color, shape) and Set size (1, 2, 4) revealed significant main effects of set size, $F(2, 40) = 44.81$, $MSE = 5.32$, $p < .001$, $\eta_p^2 = .69$, and task-condition, $F(1, 20) = 8.34$, $MSE = .71$, $p < .01$, $\eta_p^2 = .29$. An enhanced N1 was therefore found with increasing set size and enlarged N1 followed stimulus presentation in the color compared to shape condition (see Figure 10-3). The set size effect replicates the findings from Experiment 2.

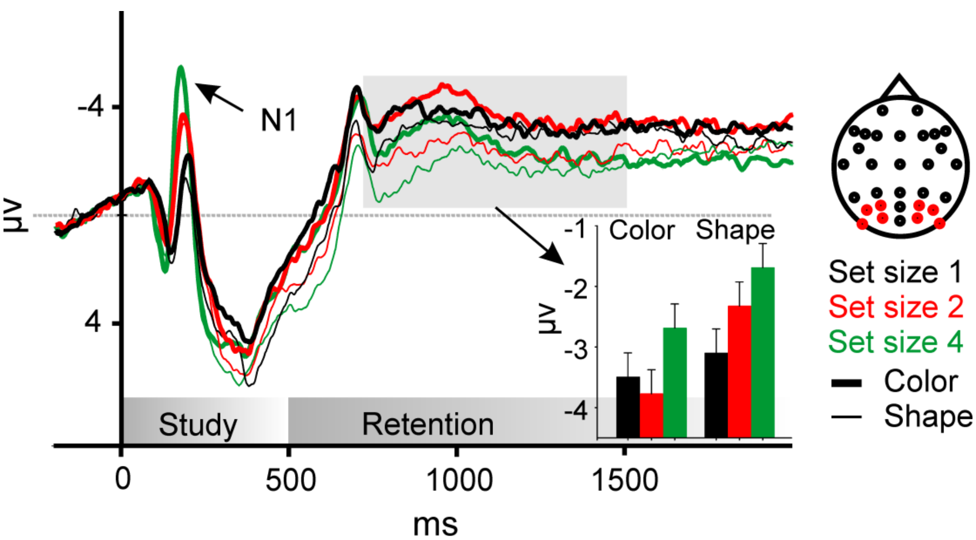

Figure 10-3. Average ERPs in Experiment 5 during study and retention at posterior cluster. Gray area indicates time window of interest (700-1500 ms). Average amplitudes are illustrated in the lower right part. Bars reflect standard errors.

Slow potentials during maintenance in the time window 700-1500 ms after onset of study display were analyzed within a posterior cluster (PO7, PO3, PO4, PO8, PO9, PO10, O1, O2) with a Task-condition (color, shape) × Set size (1, 2, 4) ANOVA (see Figure 10-3). Significant main effects of task-condition, $F(1, 20) = 11.06$, $MSE = 2.56$, $p < .01$, $\eta_p^2 = .36$, and set size, $F(2, 40) = 4.23$, $MSE = 3.35$, $p < .05$, $\eta_p^2 = .17$, were observed but no significant interaction of both factors ($p > .21$). Contrasts across task-conditions revealed no significant difference between set size 1 and 2 ($p > .45$) but between set size 2 and 4, $t(21)$

= -2,30, $p < .05$. Mean amplitudes were more positive in the shape than the color condition and more positive with larger set sizes.

10.3.3 ERPs during Target Processing

10.3.3.1 Mismatch of Task-relevant Information

For analyses of task-relevant information all set sizes were averaged and mean amplitudes in the P3 time window between 350 and 700 ms were calculated at PZ electrode (see Figure 10-4). A repeated measurement ANOVA with factors Task-condition (color, shape) × Trial type (match, non-match) was conducted. Significant main effects of task-condition, $F(1, 20) = 11.71$, $MSE = 3.83$, $p < .01$, $\eta_p^2 = .37$, and trial type, $F(1, 20) = 36.78$, $MSE = 4.44$, $p < .001$, $\eta_p^2 = .65$ were observed and no interaction between both factors ($p > .68$). P3 was larger in the shape than in the color condition and also larger in the non-match than the match condition.

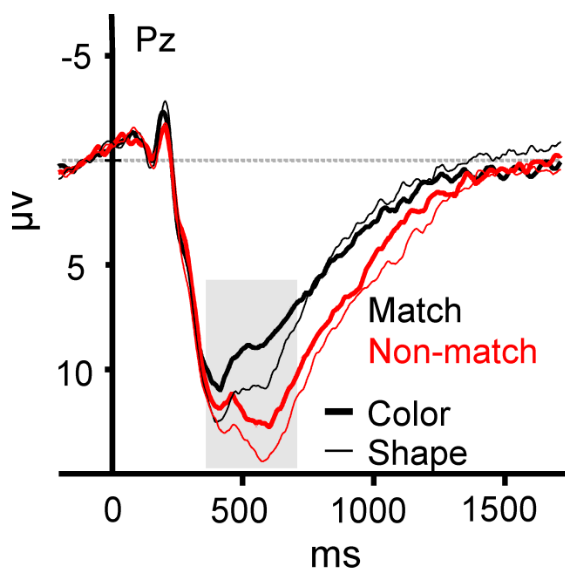

Figure 10-4. ERPs of Experiment 5 during test display at Pz electrode averaged across all set sizes. Gray area indicates P3 time window of interest (350-700 ms).

10.3.3.2 Mismatch of Task-irrelevant Information

Due to visual inspection two different time windows and electrodes were selected for analyses of task-irrelevant information in color and shape condition (Figure 10-5A). If color was relevant and shape task-irrelevant, a time window of 450-650 ms after onset of test display was selected at PO4 electrode. In the shape condition in which color was task-irrelevant, ERPs between 400 and 800 ms at CZ electrode were analyzed. Topographies of both effects are illustrated in Figure 10-6.

In the color condition, a repeated measurement ANOVA with factors Set size (1, 2, 4) and Trial type (match, change irrelevant) revealed a significant main effect of trial type, $F(1, 20) = 7.43$, $MSE = 5.58$, $p < .05$, $\eta_p^2 = .27$, and an interaction of both factors, $F(2, 40) = 5.91$, $MSE = 5.52$, $p < .01$, $\eta_p^2 = .23$. For set size 1, ERPs to change irrelevant trials went more positive, $F(1, 20) = 17.31$, $MSE = 11.26$, $p < .01$, $\eta_p^2 = .36$, whereas when two or four objects were relevant no significant effects of irrelevant shape changes were obtained ($p > .18$). A comparable analysis for the shape condition showed significant main effects of set size, $F(2, 40) = 4.87$, $MSE = 15.71$, $p < .05$, $\eta_p^2 = .20$, and trial type, $F(1, 20) = 5.91$, $MSE = 12.72$, $p < .01$, $\eta_p^2 = .39$, and no interaction ($p > .89$). It can be summarized that the difference between match and change irrelevant trials in the color condition is only significant at set size 1 whereas in the shape condition at all set sizes a significant difference between match and change irrelevant trials was observed.

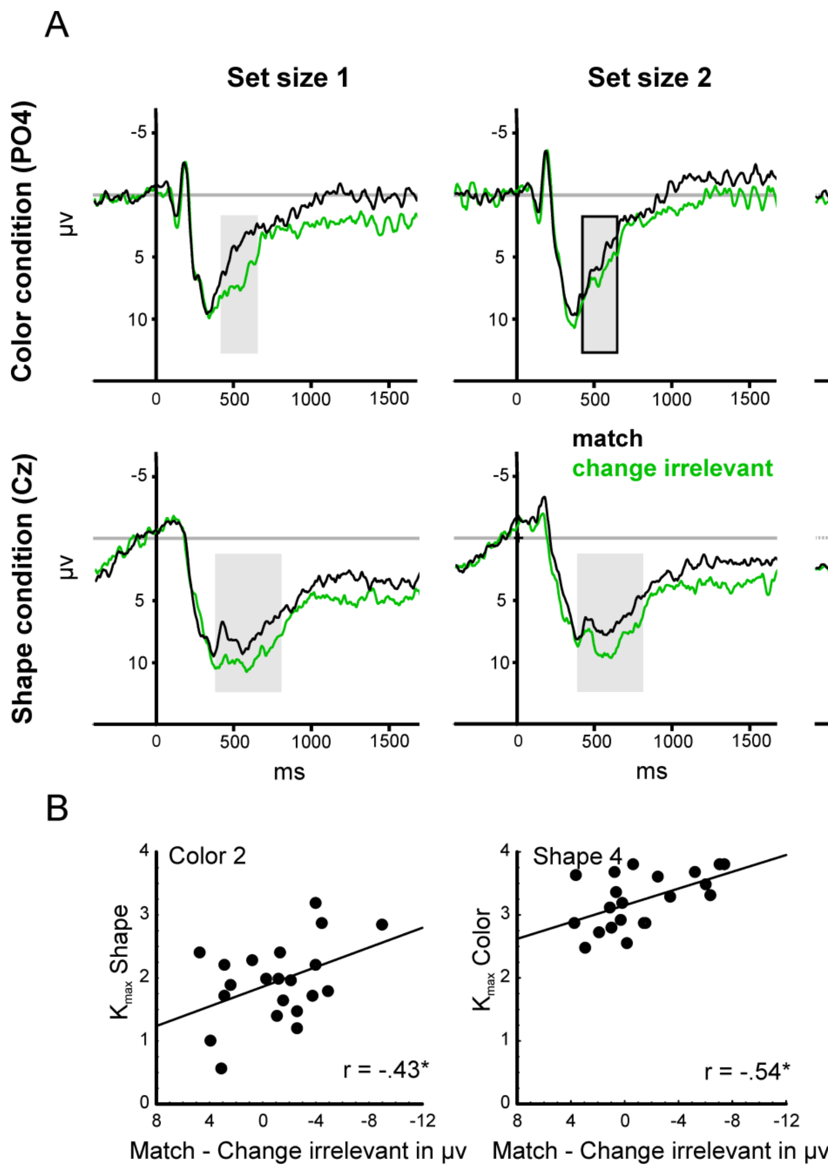

Figure 10-5. ERPs in Experiment 5 of the change irrelevant effect and its correlation with capacity. (A) ERPs for color (PO4) and shape (Cz) condition. Gray area indicate time window of interest for color condition 450-650 ms and for shape condition 400-800 ms. The black fringe at color set size 2 and shape set size 4 highlights the corresponding time window for the below presented correlation. (B) Correlation between K_{max} for shapes and the irrelevant mismatch effect in the color condition (left) and between K_{max} for colors and the irrelevant mismatch effect of shapes (right).

The mismatch effect of task-irrelevant shape information was only visible at set size 1 but not at higher set sizes, whereas a mismatch of task-irrelevant color influenced ERPs at all set sizes. This may be the case because on average only 1.9 shapes could be memorized but 3.2 colors. Non-matching irrelevant information can influence a decision only if it is memorized. Accordingly, interference of incongruent irrelevant information should disappear or get smaller if the capacity limit for this information is exceeded. Near to the average capacity limit of the irrelevant information, the interference effect should depend on the individual capacity. We assume that some participants for example can handle two shapes or more and should therefore show the change irrelevant effect, whereas others fail. If shape is irrelevant this is set size 2 in the color condition and if color is irrelevant it is set size 4 in the shape condition. To test this prediction, the change irrelevant effect was correlated with the maximum capacities of participants at these two levels. Correlations are illustrated in Figure 10-5B. Significant correlations were observed between participants' K_{max} and the magnitude of their change irrelevant effect for irrelevant shapes, $r = -.43$, $p = .05$, and colors, $r = -.54$, $p < .05$.

10.3.3.3 Topographies of Task-irrelevant Mismatch-effect

Topographies of the task-irrelevant mismatch-effect of color and shape condition are illustrated in Figure 10-6. To compensate for overall amplitude differences data were scaled according to McCarthy and Wood (1985). Then a repeated measurement ANOVA with factors Task-condition (color, shape) × Antpos (frontal, central, posterior-occipital) × Hemisphere (left, mid, right) revealed a marginal significant interaction of condition and hemisphere, $F(2, 40) = 2.65$, $MSE = .19$, $p = .08$, $\eta_p^2 = .12$. This result demonstrates that there is a tendency of lateralization of the change irrelevant effect as a function of task-condition.

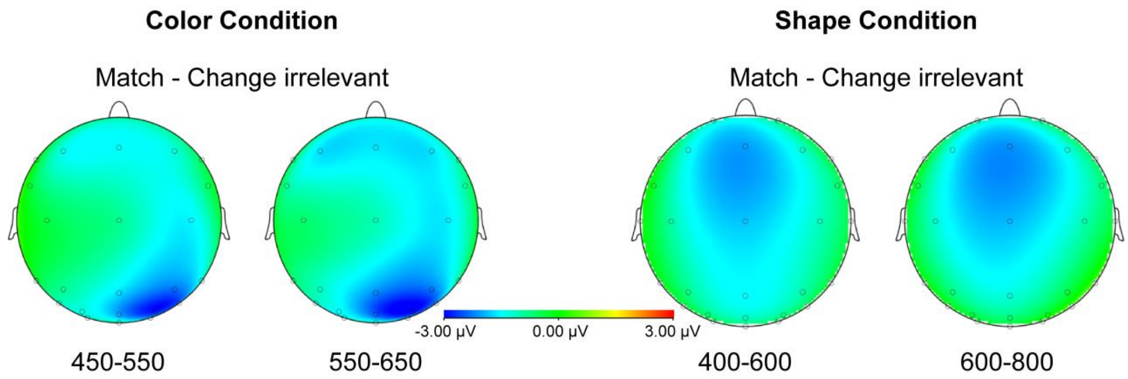

Figure 10-6. Topographies of the change irrelevant effects in Experiment 5. Time designation in milliseconds.

10.4 Discussion

The aim of Experiment 5 was to investigate the representation of task-relevant and task-irrelevant features of varying difficulty in VWM in a feature-selective CDT. For that purpose participants were required to memorize either the shape or the color of one, two or four colored polygons. The results confirmed that the color condition was less memory demanding than shape condition and memory capacity was higher for colors (3.2) than for complex shapes (1.9). Our ERP data clearly demonstrated that within these capacity limits also features with high perceptual demands seemed to be encoded even when they were task-irrelevant. As a consequence for one or two objects also their shape is represented even if it was irrelevant, if more objects were presented only color was memorized. To this result, the functional imaging data of Xu (2010) fit perfectly. She presented colored shapes in a feature-specific change detection task as we did and she provided evidence that with low memory load (set size 1 and 2) the irrelevant shape was encoded but not with high load (6 objects).

ERP effects during encoding and maintenance showed set size and task-condition effects. Slow potentials during maintenance were found to follow a more positive course with increasing set size. The overall pattern illustrates that increasing task difficulty due to task-condition and number of task-relevant objects leads to more positive going slow waves. Some studies found that slow potentials in S1-S2 tasks became more negative with increasing memory load (Mecklinger & Pfeifer, 1996; Rösler et al., 1997; Ruchkin & Canoune, 1995) whereas others could show the reversed pattern (García-Larrea & Cézanne-Bert, 1998). In line with findings from García and Cézanne-Bert, positive going slow waves with increasing set size replicates findings from Experiment 2. There however, the set size effect in slow waves was only present when shapes were relevant but not in the color condition. In Experiment 2 we interpreted the absence of set size effects within the color condition as indicator of the rather passive maintenance of color, in contrast to the more active rehearsal necessary to maintain shapes. In line with this, in Experiment 5 no increase from set size 1 to 2 was observed when color was task-relevant, but we found a clear increase to set size 4. It is possible that participants in the current experiment showed a higher task engagement compared to the former study and therefore this time actively tried to memorize four colors which exceeded their capacity for this feature. Alternatively, since task-irrelevant information was manipulated in the current study it can be assumed that in the color condition shapes were encoded additionally to ensure the probability of a correct answer. Thus a change of the task-irrelevant shape could serve as an additional clue to judge the trial type. The mental effort necessary for the attempt to encode and maintain shapes in the color condition is depicted by the set size dependent variation of slow waves during the retention interval.

Regarding performance in the color condition, neither a mismatch of the task-relevant nor a mismatch of the task-irrelevant feature had an effect. Solely the number of objects can account for a decreasing performance. A different pattern was observed in the shape condition where color was the task-irrelevant feature. Except for set size 1, performance got worse when the task-irrelevant color changed and the decrease in performance was even more pronounced when the task-relevant shape changed. Stimulus color therefore had a strong impact on memory performance even when it was task-irrelevant whereas shape did not influence performance when it was task-irrelevant. Can we interpret this behavioral data pattern as evidence for a qualitatively different processing of shape and color? Although no behavioral mismatch effect was found in the color condition clear differences between P3 amplitudes to matching and non-matching targets were observed during the test display. Change of the task-relevant color elicited an enhanced P3 compared to matching information. The same pattern was found in the shape condition. We interpret the P3 differences as bottom-up generated effects reflecting the mismatch of the displayed content and the VWM trace. It is very likely that the enlarged P3 is caused by a more complex comparison process when shapes were task-relevant.

Electrophysiological waveforms following mismatch of task-irrelevant information suggest that objects in the current task are represented including all features independent of task-condition. This is obvious in the shape condition, were a non-matching color always elicited a more positive going extended P3. In the color condition a task-irrelevant mismatch of shape modulated ERPs only when one object had to be maintained. At a glance, this seems to be consistent with the ideas provided by Gao et al. (2010) stating that easy but not difficult information is automatically represented in VWM. However, a closer look at the size of the electrophysiological correlate of non-matching irrelevant information revealed that this effect co-varied with the individual's capacity limit. This suggests that all information is encoded independent of processing demands but that different features have different capacity limits.

These capacity limits seem to depend on individuals K_{max} for the relevant feature. Strong slot models as provided by Luck and Vogel (1997) can therefore explain our results only halfway. In the object-based view it was postulated that features are always stored in an integrated way and that memory is limited by the number of objects, but not by their contents (Luck & Vogel, 1997). In line with this model is the finding that in the shape condition color information was encoded almost always. However in the color condition shapes were not always represented even though color was available which cannot be explained by object-based models. On the other hand, feature-based models are in line with the idea that memory is a flexible resource that can represent many items in coarse resolution or a few items in high resolution (Bays & Husain, 2008; Oberauer & Eichenberger, 2013). We observed that a few high-resolution features were represented and at the same time nearly twice as much low resolution features. However, we also observed that memory capacity depended on the perceptual demands of feature processing and that the two features were partially independent of each other. This observation is supported by a recent study of Bayes, Wu and Husain (2011). The authors reported that errors in a dual-feature reproduction task for color and orientation changes are independent.

When four objects were presented the number of items that can be attended is limited by the individual capacity as predicted by the slot model. This is the same number as the capacity limit for simple perceptual features, which is on average 3.2 in our experiment. However, only for a few of them difficult shapes can be successfully encoded. Since these two feature domains are independent, more colors might be represented although the maximum capacity for shapes is exceeded. Consequentially, some “objects” are represented as color only. This can explain why task-irrelevant shapes and colors had partially different effects and these effects were not symmetric. It is plausible to assume that when shapes were encoded successfully the object’s color was always represented but not vice versa.

Section 4
Final Discussion

11 Overview

In this dissertation project different measures were used to estimate costs of storage in VWM. Experiments reported in Section 2 addressed the question of information maintenance during CDT and it has been demonstrated that pupil measures and ERPs represent different aspects of cognitive processing. In Section 3 the nature of object representation was targeted by focusing on processes of the comparison between memory representation and displayed objects during test using ERPs as well. We provide new evidence about mental effort, capacity, and object representation as core components of solving a VWM task such as CDT.

12 Processes during Maintenance

One goal within this dissertation project concerns cognitive processes during maintenance of visual information in CDT. Since from past research ambiguous theories were derived about what is reflected by ERPs during retention of visual information, pupillometry was added as further measure to estimate effort. To our knowledge this is the first time using pupil measures in a visual CDT. In Experiment 1 and 2 pupil sizes were used to measure attentional effort during maintenance. Experiment 3 was conducted to further proof the idea of pupils reflecting attentional demands and Experiment 4 was planned as a control study showing the independence of obtained results from illumination. Experiment 5 was conducted to replicate ERP findings during retention from Experiment 2.

12.1 Pupils and Attentional Effort

Initially we hypothesized that pupil sizes would predict the amount of invested mental effort during maintenance of visual information in a CDT. This idea was based on early findings demonstrating that the pupil size was a suitable predictor for mental effort in digit span tasks (Kahneman & Beatty, 1966; Klingner et al., 2011; Peavler, 1974). If pupil changes reflect mental effort we further assumed that complexity of task-relevant object features should additionally impact pupils. Therefore an interaction between set size and condition was expected. In Experiment 1 we measured pupil changes during a CDT and pupil dilations were mainly found with increasing set size during the whole retention interval. As hypothesized, analysis revealed a condition × set size interaction that was based on an increasing pupil size in shape and both condition compared to color condition when two objects were task-relevant. In Experiment 2 and 3 the main effect of set size could be replicated without an additional interaction effect with set size. In Experiment 3 we additionally found a condition effect in the late time window during retention which will be discussed below.

The dilation of pupils with increasing set size fits with the results shown in past studies (Kahneman & Beatty, 1966; Klingner et al., 2011; Peavler, 1974). Changes in pupil size are associated with set size related mental effort during retention. In addition, it has been shown earlier that pupils also react to the difficulty of stimuli in language processing (Hyönä et al., 1995) or arithmetic tasks (Ahern & Beatty, 1979). Our behavioral findings in Experiment 1 and 2 suggest that the task becomes more difficult when shape rather than color was task-relevant. Performance in shape and both condition decreased beginning from set size 2 in both experiments. From these findings it can be derived that maintaining two shapes should be more difficult than maintaining two colors. As a consequence the shape condition is more difficult and should cost more mental effort. Since pupil sizes did not change with task difficulty we assume that another cognitive process such as attention is likely to evoke pupillary response in CDT.

In Experiment 2 set size dependent variations were also observed in the N1, an early negative ERP component typically apparent 100-200 ms after onset of task-relevant stimuli. As discussed in Chapter 5, the N1 reflects attention orientation to task-relevant stimuli (Luck et al., 1990). Hence, we interpreted an increasing N1 following increasing set size in the current task with enhanced attentional effort which is necessary to process the presented objects. A combined analysis with N1 size and mean pupil sizes revealed no main effect of measurement and no interaction with measurement stating that both measures are solely dependent on the number of task-relevant objects and independent from feature condition. Therefore pupil sizes in the current task are more likely to reflect attentional effort that is necessary to focus on the task-relevant objects. This interpretation is supported by findings from a multiple object tracking task by Alnæs et al. (2014). In this task participants had to focus on two, three, four, or five objects that moved around among distractor objects. Enhanced attentional effort is thus necessary to follow an increasing number of objects. The authors clearly showed that pupil size is a function of the number of tracked objects which was interpreted as the amount of attentional effort (Alnæs et al., 2014). In this study they further showed that pupillary activity predicts activity within the LC which was taken as further evidence for the integrated pupil-LC approach (Alnæs et al., 2014). Our results are in line with these findings, and suggest that pupil sizes reflect the engagement of attentional effort to process task-relevant information.

In Experiment 3 we provided additional evidence that pupils rather reflect attention than encoding or maintenance processes. The main difference between the first two experiments and Experiment 3 is the extension of using a cue to inform participants beforehand about the number of to be maintained objects. Therefore participants could prepare during the CTI for the following study display. Although the visual input during cue presentation was the same – because black digits from 1-5 were used, pupil sizes differed across set sizes. Increasing pupil sizes were observed when four or five objects were cued compared to lower set sizes. Since no encoding or maintenance processes take place during CTI, pupil changes during that phase of the trial are likely the result of enhanced attention that was directed to the task when more objects were task-relevant. During the retention interval the attention effect became large as a strict function of set size which replicates findings from Experiment 2. Interestingly, condition affected pupils in the late time window of the retention interval in Experiment 3, which was not observed in Experiment 1 and 2. Hence, when the more complex shape was task-relevant an increase of pupil sizes was observed compared to the color condition. We can only speculate about the presence of this condition effect in Experiment 3 and its absence in the previous studies. A possible explanation could be that the pupillary response during retention in principle contains both, processes of maintenance effort and processes of attentional effort. Since no cue helped participants to prepare for the study display in Experiment 1 and 2 it is therefore likely that maintenance effort is superimposed by attentional processes. When set size was cued, parts of the attentional processes were relocated to the CTI and maintenance effort was visible more clearly during the retention interval. Nevertheless, this interpretation is speculative as it lacks additional information and further research would be necessary to unravel this pattern.

A frequently discussed topic in terms of cognitive driven pupil effects is its sensitivity to changes in luminance. Experiment 4 was conducted to demonstrate the independence of our pupillary findings in the previous three experiments from illumination caused by the colored polygons. Pupil size did not increase with set size in Experiment 4 which can be taken as evidence for our observed pupil changes reflecting cognitive operations in Experiments 1-3.

Another observation in Experiment 1-3 is a general increase of the pupil diameter across the retention interval (see Figures 4-4, 5-2, and 6-3) and in Experiment 3 during the CTI as well (see Figure 6-3). It is visible that pupils' diameter slightly increase during the whole retention interval. It has been demonstrated that pupil size is influenced by response preparation processes (Moresi et al., 2008). The authors showed that after presentation of a cue pupil became more positive until presentation of the stimulus. Further, increasing pupil diameter was observed between stimulus and response (Moresi et al., 2008). Similarly, the overall pupil course in Experiment 1-3 can be interpreted as response preparation processes.

12.2 ERPs and Mental Effort

A considerable body of work demonstrated that slow ERPs during retention of visual information simply reflect the number of objects until capacity maximum is achieved (e.g. Luria & Vogel, 2011; McCollough et al., 2007; Vogel & Machizawa, 2004). In parallel others challenged this view by showing that feature complexity influences slow ERPs during retention (Gao et al., 2013; Luria et al., 2010; Woodman & Vogel, 2008) suggesting that effort necessary to store visual information is as well reflected by slow waves. In line with the latter view we used slow waves in the CDT to estimate the amount of cognitive effort in different set sizes and conditions.

In Experiment 2, performance in shape and both condition dropped when two or four objects were task-relevant compared to the color condition. Slow waves and the posterior P2 during retention - as found in performance data - behaved the same way in both and shape condition and thus differed from the color condition. When shape was task-relevant (shape, both) slow waves and P2 became more positive with increasing set size whereas no difference between sets sizes was found in the color condition. This pattern does not fit to number-of-objects theories as provided by Vogel and Machizawa (2004). There, increases of the CDA were observed with the number of stored objects until the capacity maximum was achieved. In Experiment 2, slow waves increased during shape condition linearly with set size although a K_{max} of almost two objects was revealed. Thus, when slow waves reflect the number of stored objects, no difference should be present between set sizes 2 and 4. The same argument is true for slow waves during the both condition. The absence of any ERP differences in the color condition as well is evidence against the number-of-objects theory. We therefore interpret slow waves during retention to reflect mental effort elicited by the complexity of task-relevant features. As shown by Woodman and Vogel (2008) the CDA during retention increased when complex orientation of objects was task-relevant compared to objects' color. This suggests that the nature of task-relevant features impacts ERPs during retention as we found in Experiment 2. When shape was task-relevant storing more objects led to higher effort costs. This pattern was absent in the color condition. In an open questionnaire following the experimental session we asked participants about their strategies of solving the task and a joint answer was that the maintenance of colors "happened passively" whereas shapes were tried to "maintain actively". Basically these oral statements best explain the slow wave results. Differences in mental effort were observed between set sizes when shape was task-relevant whereas "passive" maintenance in color condition was observed regarding the slow waves.

The posterior P2 probably reflects the initial processing of task relevant stimuli (Gevins et al., 1996). Interestingly, a very similar effect was observed in a completely different task in which only one item was memorized but this item varied in visual complexity (Liesefeld & Zimmer, 2013). In this task participants were required to encode one artificial shape and then to mentally rotate it. A visually more complex shape caused more positive waveforms during encoding which looked very similar in the P2 time window. These effects are therefore very likely effects of encoding more complex stimuli.

We could replicate ERP findings from Experiment 2 in Experiment 5 partially. Although experimental modifications such as the manipulation of task-irrelevant information and the omission of the both condition were implemented, we can assume that maintenance processes in color and shape condition during retention are comparable between both experiments. In Experiment 5 main effects of condition and set size were observed in slow waves. In general positive going slow waves with increasing set size were found and slow waves in the shape condition were more positive compared to the color condition. It seems that at least when four objects were task-relevant maintenance in the color condition showed higher effort costs compared to set sizes 1 and 2 which was not present in Experiment 2. However, the pattern in the shape condition was found to be the same as in Experiment 2. When we interpret slow waves during retention of visual information in terms of mental effort, the implications of both experiments are the same: (1) maintaining color is less effortful than maintaining shape and (2) especially in the shape condition effort is moderated by set size.

13 Processes during Test

A second goal of this dissertation project was to investigate the nature of object representation in VWM. Clear conclusions about what is represented in VWM can be drawn from measures that determine ongoing processes during the test display in CDT. Therefore in Experiment 5 we manipulated in addition to task-relevant information also task-irrelevant information, to gain information about selective storage of features in VWM.

13.1 Behavioral Implications

The pattern of behavioral findings in terms of VWM capacity (color > shape) in Experiment 5 was nearly the same as in our previous experiments: participants were able to maintain 1.9 objects when shape was task-relevant and 3.2 objects when color was the task-relevant feature. Interestingly, an interaction of task-condition and trial type was also observed for task-irrelevant information, suggesting that the manipulation of task-irrelevant information differentially affected memory accuracy. As expected, performance in the color condition dropped with increasing set size but no differences between trial types (match, non-match, change irrelevant) were observed. Therefore, the performance pattern in the color condition does not give rise to assumptions about processing of task-irrelevant shape (i.e. changes of task-irrelevant shape information produces a conflict between memory representation and displayed information). When four items were task-relevant in the color condition the difference between trial types was marginally significant but the difference between match and change irrelevant trials did not reach significance (see Figure 10-2A). In contrast, performance in the shape condition clearly decreased when the task-irrelevant color was manipulated. Performance in the change irrelevant trials dropped compared to match trials. It is important to notice that in match and change irrelevant trials participants had to press the “no change” key. Solely a change of the irrelevant feature impaired performance when two or four objects were presented in the shape condition.

Studies conducted by Gao et al. (2010) mainly stated that changes of irrelevant information affected ERPs during test only when it was salient information. In the majority of their studies only one object was presented and performance was unaffected by manipulation of the task-irrelevant information. In their last experiment, however, set size varied (set size 1, 3). Here, at set size 3, performance decreased when task-irrelevant shape information was manipulated which was the salient feature (Gao et al., 2010). We were able to replicate this finding by showing that changes of task-irrelevant features impair performance only when the changed information is salient and when more than one item is task-relevant.

Our behavioral data suggest that color as salient feature is processed automatically and can impair performance even when it constitutes task-irrelevant information. In contrast, in the color condition task-irrelevant shape information did not affect performance, suggesting that it is not processed automatically and only represented in VWM when it is task-relevant. Therefore, whether features can be stored selectively seems to depend on their salience.

13.2 Electrophysiological Implications

ERP waveforms during retention of visual information were already discussed in detail in Chapter 12.2 in the context of mental effort. In this chapter we now focus on ERP results during the test display in Experiment 5. In general, the results indicate that the manipulation of information from study to test display modulates ERPs following onset of the test display in the P3 time window. We observed positive going waveforms when task-relevant and task-irrelevant information was changed compared to match trials.

As illustrated in Figure 10-3, changes of task-relevant information elicited an enhanced P3 across all set sizes (non-match > match). This P3 enhancement was generally larger in the shape condition compared to color condition (shape > color). However, in the color condition a significant P3 difference between match and non-match trials was found although performance between these trial types did not differ. Likewise, such a P3 modulation was found in the shape condition correspondent to performance. As Kok (2001) outlined, the P3 amplitude is modulated by the activation of elements in a categorization network. This suggests that elements of the memory trace were compared with the content of the study display and thus modulated the P3 amplitude. The observed ERP match - non-match effect in Experiment 5 therefore supposedly reflects a bottom-up detection of a mismatch between memory representation and display content. Nevertheless, since larger amplitudes in the shape condition compared to the color condition were found, although visual input in both conditions was identical, top-down mechanisms were likely to influence P3, too. The only difference between conditions was that a different kind of stimulus attribute was task-relevant and hence participants shifted their focus of attention to the respective task-relevant feature. In an early study by Ullsperger et al. (1988) it was shown that the P3 amplitude depends on the demands of memory operations. Larger P3s were observed with increasing memory demands (Ullsperger et al., 1988). This finding is in line with our results stating that amplitude of P3 increased when shape was task-relevant compared to the color condition. This enhanced

P3 is likely to be caused by a more demanding comparison process between memory representation and displayed content in the shape condition.

As we discussed in Chapter 9.2, Gao et al. (2010) reported a N270 that varied with changes of task-irrelevant information in S1-S2 tasks. Solely changes of highly discriminable information elicited an enhanced N270, whereas changes of more complex features did not modulate N270. The authors provided a model suggesting that the extraction of coarse information into VWM occurs automatically whereas fine grained information has to be extracted intentionally (Gao et al., 2010). In Experiment 5 no such N270 modifications were observed during the test display. The most obvious difference between the few N270 studies (Gao et al., 2010; Yin et al., 2011) and the present study is that we varied set size, whilst in the former studies only one item was used or at least a fixed number of objects were task-relevant with no variation of set size (Zhou et al., 2011). Another difference between these studies and Experiment 5 concerns the timing within the trial course. Gao et al. (2010) presented the study information for only 200 ms and used a 1000 ms retention interval whereas in the current study we used a presentation time of 500 ms and a 1500 ms retention interval. We can only speculate about reasons why no N270 modulation was present in our design, but operational differences, such as timing differences and variation of set size, might be responsible for a lack of N270 in Experiment 5.

Indeed, no N270 was present, but we found a modification of ERPs during the late P3 time window that was not observed in previous studies (Gao et al., 2010; Yin et al., 2011). In the color condition a change of the task-irrelevant shape elicited positive going waveforms between 450 and 650 ms at right posterior sites compared to match trials. In the shape condition, a change of the task-irrelevant color provoked a positive waveform between 400 and 800 ms at central electrodes compared to match trials. Although topographical analyses did not reveal a significant difference between these two effects, which points to the involvement of similar underlying processes, there was trend towards a right hemispheric lateralization of the irrelevant shape effect. ERP differences were observed although the correct response in both trial types (match, change irrelevant) was the same, that is “no change”. The fact that a more positive going ERP waveform was present in the change irrelevant trials can be taken as evidence that task-irrelevant information is represented in VWM. Interestingly, our results show an ERP effect for both kinds of task-irrelevant feature, whilst in previous studies effects of task-irrelevant information were observed only for salient information (Gao et al., 2010; Yin et al., 2011; Zhou et al., 2011).

Furthermore, the idea that the ERP effects following mismatch of task-irrelevant information are based on its representation in VWM is further supported by a correlation of this effect with individuals’ maximum capacity. This correlation states that participants with high VWM capacity show a negative match – change irrelevant difference, whereas participants with low VWM capacity show a positive ERP difference (see Figure 10-5B). Since maximum capacity in the shape condition was 1.9 and 3.2 in the color condition, ERP differences of the change irrelevant effect in set size 2 in the color condition and in set size 4 in the shape condition were respectively used for each correlation. The correlation clearly asserts that information is represented in VWM regardless of its task-relevance and salience. Participants with higher VWM capacity showed a larger ERP difference between match and change irrelevant trials which can be taken as evidence that this effect reflects the critical feature representation. Since the change irrelevant effect appeared during the test display the ERP difference is unlikely to constitute e.g. enhanced effort of high capacity participants. Our data lead to the conclusion that the presence of the change irrelevant effect simply can be equated with the successful representation of the irrelevant feature.

From findings during test display in CDT the following conclusions can be drawn: (1) performance is affected by change of task-irrelevant information only if the irrelevant feature is salient (color). (2) P3 differences during the test display revealed a dependency on condition and trial type (match, non-match) suggesting enhanced P3s following mismatch of task-relevant information and more difficult comparison operations. (3) The change irrelevant effect in ERPs is independent of feature salience and is apparent until the individuals' capacity maximum is achieved.

14 Implications in Terms of Object Representation

In Chapter 1.3 two influential models were discussed making assumptions about how objects are represented in VWM. The object-based view was introduced and supported by Luck and Vogel (1997) and its core prediction is that VWM capacity is limited by the number of objects only. In contrast the feature-based view (Bays & Husain, 2008; Olson & Jiang, 2002) was motivated by the finding that the number of features per object sets the capacity limit in VWM. In Chapter 1.4 a third model was introduced holding the idea of objects being represented in hierarchical feature bundles (Brady et al., 2011). This model was developed as a consequence of different findings stating that capacity may vary with the type of task-relevant feature. We discuss the implication of our data on these models below.

14.1 Object-based Models

Within the object-based view it is explicitly assumed that a varying number of features can be integrated in one object and therefore stored in a slot in VWM without additional costs on capacity (Luck & Vogel, 1997; Vogel et al., 2001). A further assumption is that feature complexity does not influence memory capacity (Awh et al., 2007). Behavioral data in Experiment 1-3 and 5 were not consistent with the object-based view. We observed decrease of performance dependent on the type of task-relevant feature. Accordingly, performance dropped when shape was task-relevant which was represented in the K-indices as well: in all experiments capacity in the shape condition varied around 2 objects whereas in the color condition approximately 3 objects could be maintained.

It was further demonstrated that maintenance of some of the features used in the original experiment by Luck and Vogel (1997) such as orientation of objects was more memory demanding than others (e.g. color of objects) (Woodman & Vogel, 2008). Our ERP results during retention of visual information in Experiment 2 are consistent with this idea. We observed variations of slow waves dependent on task-condition that emerged as more positive going waveforms with increasing set size when shape was task-relevant, but not when color was task-relevant. Slow waves varying with set size in the shape and color condition were observed in Experiment 5 as well. As discussed in Chapter 12.2 slow waves during a CDT reflect mental effort that is necessary to process task-relevant features. This finding is basically not incompatible with object-based models. A substantial argument for the calculation of the CDA was that task-related effort has an impact on bilateral slow waves during retention (Vogel & Machizawa, 2004). Therefore it is possible to unify the idea of slot-organization of VWM and varying memory demands dependent on task-relevant features.

In Experiment 5 we showed that also task-irrelevant information is represented in VWM until the individuals' capacity maximum for a given feature is achieved. From an object-based view we would assume that when an object is represented, all features are accessible. In contrast when an object is not represented, no information should be accessible then. When a participant in Experiment 5 could successfully maintain two shapes, how can we explain the concurrent representation of three colors? Electrophysiological data during test stated that pure object-based representation is unlikely in the current design.

As a summary it could be demonstrated from behavioral data that VWM capacity highly depends on the complexity of task-relevant features. ERPs during test display clearly exhibited that the amount of features which are represented individually is a function of their complexity. These findings are not compatible with the "all-or-nothing" assumption that is made by object-based models of VWM.

14.2 Feature-based Models

A core assumption of feature-based models is that not the number of objects, but the number of features per object (Bays & Husain, 2008; Oberauer & Eichenberger, 2013; Olson & Jiang, 2002) and/or the features' complexity (Song & Jiang, 2006) are the capacity limiting factors in VWM. Behavioral data of Experiment 1 and 2 revealed a complexity effect when shape was task-relevant but no differences between shape and both condition. Feature-based models would predict a decreasing performance when both features were task-relevant compared to the shape condition. Our performance data rather suggest that color is stored automatically in the both condition without any additional costs. The complexity effect was clearly observed in Experiments 1-3 and 5 which replicates findings by Song and Jiang (2006).

Slow waves during retention did match our idea of a more demanding maintenance process of complex features and underlines behavioral findings regarding feature complexity. Enhanced mental demands during maintenance of complex information are in line with the feature-based view which predicts that capacity limits are a function of feature complexity (Oberauer & Eichenberger, 2013). Demanding characteristics were observed especially when shape was task-relevant.

ERPs during the test display in Experiment 5 are difficult to explain within the feature-based approach. Results after manipulation of task-irrelevant information revealed that color and shape are always represented in VWM regardless of the task-condition. This implies that feature representation is an automatic process at least in our design. In the color condition, objects' shape was always represented until maximum capacity for shapes was reached. The same was observed in the shape condition, where the objects' color was represented. We could not show costs for storage of the task-irrelevant feature in Experiment 5; it rather seems to be represented automatically. This observation contradicts the feature-based model since no dependency between the number of colors and the number of shapes that can be successfully represented was observed. Both features seem to be represented without influencing each other.

Results of the current experiments are not fully explainable by feature-based models. Complexity effects in performance and in slow waves basically support the idea of feature-based representations in VWM but the lack of a difference between the shape and both condition does not fit into a feature-based explanation of the present data. Both features of the objects we used in the current experiments were represented independent of the task-condition, as indicated by ERP findings in Experiment 5. From these findings we cannot conclude that VWM capacity is limited by the number of features per object. Our data suggest an automatic storage process of all features dependent on the individual VWM capacity.

14.3 Hierarchical Feature Bundles

As already discussed in Chapter 1.4 an alternative model about how objects are represented in VWM was elaborated by Brady et al. (2011). As an extension to object- and feature-based models, the authors suggest a representation of items on both the object and the feature level. The critical component of this model is that an initial object-based representation is created and on lower levels of this representation feature information is stored (see Figure 1-1) (Brady et al., 2011). Importantly, this feature-information can be present or absent. The idea that objects are organized as hierarchical feature bundles fits well with the data obtained in the present work. As already discussed in the previous chapters, it remains unclear why three colors were represented in the shape condition and two shapes were represented in the color condition. Our results of Experiment 5 might be best explained in light of assumptions from Brady et al. (2011), who supposed that initially an object representation is created and attached to this initial representation features are represented adequately. The initial object representation can thus serve as a frame where feature information is optionally attached. The model of hierarchical feature bundles is also consistent with findings that slow waves during retention reflect mental effort elicited by the task-instruction.

15 Conclusion

The first goal of this dissertation was to investigate costs of maintenance in VWM within a CDT. Therefore, pupil sizes and ERPs were used as online measures to gain insights in ongoing cognitive processes. Changes in pupil size were demonstrated to depend on the number of objects und were interpreted in terms of effort, which is necessary to direct attention to task-relevant items. The same pattern of results in the N1 component, which is associated with attentional demands as well, supported this interpretation. Pupil changes were further shown to be independent of illumination differences elicited by the colored polygons. In contrast, slow waves measured during retention of visual information were highly dependent on task-condition and set size and thus interpreted to show mental effort that is needed to process task-relevant features. As exhibited in Experiment 3 pupil dilation also seems to display effects of task-condition which requires further investigation.

The second goal of this project was to further figure out how objects are represented in VWM. For this purpose task-irrelevant information was manipulated and ERPs were recorded during test display of a CDT. Changes of the task-irrelevant color or shape elicited a mismatch effect which can be taken as evidence that all features of the presented objects are represented independently of its salience and task-relevance. The correlation of this electrophysiological mismatch effect with maximum capacity of the respective feature demonstrates that even representation of task-irrelevant information depends on its capacity limits. Our data fit well with the VWM model of Brady et al. (2011) suggesting that visual information is represented in both the object- and the feature dimension.

16 References

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