FACULTEIT PSYCHOLOGIE EN PEDAGOGISCHE WETENSCHAPPEN

The influence of auditory and contextual representations on visual working memory

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Do. Or do not. There is no try.

Yoda, 1980

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I made it! This is the last thing I will write for my dissertation, the acknowledgements. Some say it is the best part of a thesis (probably because it is the only part that most people will read), others think it is nonsense (I'm looking at you E.A.). I think it's neither the best part, there is some amazing stuff further on if you dare to read beyond this part, or nonsense, nobody can do this alone and people need to be thanked.

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Michel,

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Chapter 1
Introduction

Working memory is our ability to maintain a limited amount of information for a brief period of time, even when that information is no longer physically present. While this ability seems fairly simple and straight forward, it allows us to do a wide variety of complex tasks and activities. To illustrate, imagine you are on the side walk of a busy street. You are hungry and decide to buy a sandwich at a shop across the street. To get the sandwich, you will need to cross the street, enter the shop, and buy the sandwich. To cross the street you need to keep track of traffic around you: cars are approaching from left and right and other people are walking on the sidewalk in all directions. You look to your left and see a car approaching; simultaneously you hear the siren of an ambulance in the distance approaching from the right. At this point in time you are actively maintaining and keeping track of; the car approaching from the left, the ambulance approaching from the right, the goal of buying a sandwich, and the plan to cross the street and enter the shop to buy it. It is easy to see how failures of working memory can lead to problems in daily life. It is therefore no surprise that working memory, and its related processes, is at the forefront of research in human cognition.

The information we maintain in working memory comes from a wide variety of sources: sensory information (i.e., the visually perceived car or auditory perceived ambulance), motor action information (i.e., the planned action to cross the street), and long-term memory (e.g., the concepts “street”, “car,” “ambulance”, and “sandwich shop”). So besides the short-term maintenance of information, the integration of information from multiple sources and the creation of a coherent representation of our external world are an important aspect of working memory. Despite the importance of integrating and creating such a coherent representation, research has mostly focused on the storage aspect of working memory. How information is integrated and represented in working memory is the central theme of this dissertation. The first part of the current dissertation (Chapter 2 and Chapter 3) examines how visual information is integrated and represented in working memory. The second part (Chapter 4 and Chapter 5) explores how information from different senses and long-term memory representations can interact or integrate with each other.

A brief history of Working Memory Research

Ever since psychology established itself as an independent scientific discipline, researchers have turned their attention toward human memory. Much of this early research compared human memory to a library in which information could be encoded and stored, and from which information could also be retrieved. In essence, this early research thrived on using a library metaphor of human memory, which resulted in a strong focus on the encoding (and subsequent forgetting) of information in memory (see e.g. Ebbinghaus, 1885). Moreover, most researchers at that time considered memory to be a single system and it was not until the late 1950s that memory was thought to consist of having multiple stores, out of which one was dedicated to the temporary storage of information (e.g., Broadbent, 1958; Brown, 1958; Peterson & Peterson, 1959).

Based on the ideas of that time, Atkinson and Shiffrin (1968) devised a model for the flow information through multiple components in human memory, later known as the modal model. In their seminal work, they suggested that environmental information is processed in parallel by various sensory registers, (one for every modality, e.g., visual, or auditory) before they are combined and transferred into a short-term store. From the short-term store, information can enter long-term memory, which is considered to be a permanent store without any capacity limits. Atkinson and Shiffrin (1968) regarded the short-term store to be a fundamental property of information flow in human memory, which set the modal model clearly apart from earlier attempts to explain human memory. According to the model, information that enters the short-term store can be retained for a limited amount of time determined by a set of cognitive control processes that are assumed to be under a person's voluntary control. These control processes are encoding, rehearsal, and retrieval. For example, the contents of the short-term store can be copied to the long-term store by way of continuous rehearsal of these contents. Moreover, information related to the content in the short-term store might be activated in the long term store and reenter the short-term store, by means of a retrieval process. It is this active manipulation of information in the short-term store that defined the term "working memory" as it was obviously more than just the passive storing of said information.

Atkinson and Shiffrin's modal model has been influential for a long time. Because of its clear structure and mathematical nature the model was well equipped to make specific predictions for many different paradigms. The rigid architecture of memory systems as suggested by Atkinson and

Shiffrin (1968) could, however, not account for the apparent flexibility of memory systems observed in for example: learning (e.g., Craik & Lockhart, 1972), neuropsychology (e.g., Shallice & Warrington, 1970), and item categorization (e.g., Crowder, 1979).

Several years later, Baddeley and Hitch (1974) proposed a multiple component model of working memory, which was better equipped to explain the flexibility of memory systems. The main component of this model is the central executive, which is assumed to focus attention, to update working memory contents, and to provide a link to long-term memory. This central executive is assisted by two domain-specific subsystems: the phonological loop and the visuo-spatial sketchpad. The phonological loop is used for short-term maintenance of speech-based and acoustic items and the visuo-spatial sketchpad maintains visually and/ or spatially encoded items. The separation of working memory storage in a verbal phonological loop and a nonverbal visuo-spatial sketchpad was based on converging evidence collected from research with brain-damaged patients, and research with dual-task paradigms in healthy patients (Baddeley & Hitch, 1974). First, specific patterns of brain damage can show impaired memory for verbal material while memory for nonverbal material stays intact (e.g., Shallice & Warrington, 1970; Vallar & Papagno, 2002), and vice versa (e.g., Della Sala & Logie, 2002). Second, these patterns can be imitated with a dual-task paradigm and this method has successfully shown that memory for verbal material did not interfere with memory for visual information and vice versa (e.g., Cocchini, Logie, Della Sala, MacPherson, & Baddeley, 2002; Logie, Zucco, & Baddeley, 1990). The basic premise of this type of research is that if two processes use the same underlying system they will compete for processing resources, which will cause interference and a degradation of performance. Likewise, if two processes do not share a single underlying system, there will be no interference and hence no performance cost.

The clear separation of the phonological loop and visuo-spatial sketchpad could, however, not hold up, due to the fact that evidence showed more interaction between the two systems than the original model would suggest. A fourth component was added to this model to account for the interactions between the two slave systems. This system, the episodic buffer, acts as a link between the two subsystems, and provides a link between long-term memory and the central executive. It is a storage system that can hold about four chunks of information in a multidimensional code. The episodic buffer integrates different memory codes into a coherent perceptual scene, including e.g., auditory, visual, tactile, or olfactory information (Baddeley, 2000). Although the episodic buffer can in theory explain a lot of the interactions found between the different slave systems, attention, and long-term memory, and could even help to bridge the gap between research in working memory and multisensory integration (see Chapter 5), it is by far the least examined component of the working memory model.

Although the above-discussed models are not as prominent in the field of cognitive science anymore, they did introduce the basis for many of the concepts and structures that still hold up to this day. Both models capture the essential role of working memory in information processing that is used to guide complex behavior. Moreover, both models touch on the integrative aspect of working memory. Atkinson and Shiffrin's model (1968) assumes that information from different senses is recoded in an amodal (modality independent) form for subsequent maintenance in the short-term store. In

Baddeley and Hitch's model, modality specific information is integrated to create a coherent perceptual scene in the episodic buffer (Baddeley, 2000). Both models assume that information is maintained in a specific passive store or buffer and that attention is used to control what enters and exits the store. Recent working memory models have emhapsized this integral role attention in working memory encoding, maintenance, and retrieval much more prominently (e.g., Awh, Vogel, & Oh, 2006; Cowan, 1988; Oberauer, 2009). Indeed, some of these models suggest that working memory and attentional processes might be the same, or part of a mutual underlying system (Olivers, 2008; Kiyonaga & Egner, 2013; Postle, 2006). The critical difference between these attention based models and the before mentioned storage models is that the maintenance of information is achieved by sustained attention to relevant information instead of information being put in a passive storage component.

To summarize, working memory is a complex framework of multiple interacting processes that involve the temporary maintenance and manipulation of information that guides complex cognitive behavior. After the initial perception of sensory information, a small amount of this information can be actively maintained for a brief period of time. Similarly, long-term memories can be activated for active manipulation through various control processes. Attention seems to play an essential role in keeping information active in memory. Although the interaction or integration of multiple sources of information in working memory seems an important part, working memory models and research have largely focused on examining the sources of information separately.

VISUAL WORKING MEMORY

One of the defining characteristics of working memory is its limited capacity, that is, the limitation in the amount of information a person can maintain at a time. There are large individual differences in working memory capacity and these differences have been shown to correlate with a large number of factors, including fluid intelligence (Conway, Cowan, Bunting, Therriault, & Minkoff, 2002; Engle, Tuholsky, Laughlin, & Conway, 1999; Fukuda, Vogel, Mayr, & Awh, 2010), reading comprehension (Daneman & Carpenter, 1980), and academic achievement (Alloway and Alloway, 2010). Thus, understanding the limits of working memory capacity can be important in gaining insights in general cognitive functioning. Indeed, research over the years has focused on finding the limits of working memory capacity.

One of the first to investigate the capacity of working memory was Miller (1956). In his seminal paper, “The magical number seven, plus or minus two”, Miller has described the limitations found in absolute judgement and immediate memory span tasks. While Millers’ paper specifically concerned the recoding and grouping of information in what he called ‘chunks’, he also mentions his fascination with what seems to be a returning number of on average seven items that can be maintained or attended to at the same time. Since then, considerable research has shown a constant capacity limit in a wide variety of tasks, although this limit is closer to four instead of Miller’s suggested seven (see for a review: Cowan, 2001). One important question is then: how does this capacity limit come about?

Visual working memory capacity limits

This has been one of the questions driving research in visual working memory, our ability to temporarily maintain a representation of visual items in memory without the physical presence of these items. Research on visual working memory has led to two competing ideas that can explain capacity limits. The first idea is that capacity is limited by a fixed number of integrated objects that can be maintained regardless of the amount of visual information per object (Cowan, 2001; Luck & Vogel, 1997; Zhang & Luck, 2008). The second idea, in contrast, is that capacity is limited by a fixed amount of visual information, regardless of whether this information is distributed among multiple objects or not (Alvarez & Cavanagh. 2004; Bays & Husain, 2008; Wilken & Ma, 2004). Over the years support has been found for both models and is the reason why this is a major point of discussion in the visual working memory literature.

Visual working memory capacity has mostly been investigated by using the so-called change-detection task. In this task, participants are presented with a memory array containing one or more visual objects, which they have to maintain in memory for a brief period of time. Then participants are again presented with an array containing one or more of the objects and they have to indicate whether a change has occurred, compared to the memory array. When the number of presented objects is low compared to an individual's capacity limit, performance will be near perfect. When the number of objects presented exceed an individual's capacity limit, performance will deteriorate systematically with each added object.

Using a change-detection task Luck and Vogel (1997) were among the first to examine visual working memory capacity for visual objects. They found that participants could maintain up to four objects in working memory without much difficulty but that performance declined fast when the number of items increased beyond four, regardless of the amount of visual information that had be memorized per object. These findings were the basis for what is known as the “slot” or discrete resource model of capacity (Cowan, 2001; Luck & Vogel, 1997; see for a review: Luck and Vogel, 2013). This model assumes that a person’s capacity is limited by a fixed number of objects he/she can maintain simultaneously in working memory, which can vary slightly from person to person (Vogel & Machizawa, 2004). When the number of items that need to be memorized exceeds the number of “slots” available, a subset of items will be stored in an all or nothing approach, meaning either all of the information of one object is stored or nothing. This view has been supported by a large number of studies (Anderson, Vogel, & Awh, 2011; Aw, Barton, & Vogel, 2007; Ikkai, McChollough, & Vogel, 2010; Scolari, Vogel, & Awh, 2008; Vogel & Machizawa, 2004; Vogel, Woodman, & Luck, 2001; Zhang & Luck, 2008). Most of these studies used a typical change-detection task with a binary response, meaning participants indicated whether a change had occurred yes or no. A limitation of this approach is that it is impossible to make any assumption on the precision with which each item is memorized. Simply put, are mistakes in the task made because the target object was not in memory, or because the representation of the target object in memory was not precise enough to clearly perceive a change?

An alternative to the discrete resource or “slot” models is provided by the continuous resource models (see for a review: Ma, Husain, and Bays, 2014). These models propose that a single memory resource can be distributed evenly among visually presented items and that an increasing number of items can be memorized at the cost of the precision or resolution of that item. Strong support for these models has come from studies employing a continuous report task, a variation of the change detection task. Instead of giving a binary response (a change has occurred; yes or no) participants are required to reproduce one of the items in memory on a continuous scale. By examining the discrepancy between the presented item and the item reproduced from memory, an estimate of the precision of that item's representation in memory can be obtained. Indeed, studies that have employed this method generally find that the discrepancy between the presented item and reproduced item increases as a function of the number of items that have be memorized (Bays, Catalao, & Husain, 2009; Bays, Gorgoraptis, Wee, Marshall, & Hussain, 2011; Bays & Husain, 2008; Fougnie, Cormiea, Kanabar, & Alvarez, 2016; Wilken & Ma, 2004). This indicates that there is a possible trade-off between the number of objects and the precision with which these objects can be stored.

More evidence against the view that visual working memory capacity is limited by a fixed number of discrete "slots" has been accumulated. For example, research has shown that the visual complexity of items can influence the maximum number of items that are stored in memory (e.g., Alvarez & Cavanagh, 2004; Diamantopoulou, Poom, Klaver, & Talsma, 2011; Eng, Chen, & Jiang, 2005; Luria, Sessa, Gotler, Jolicoeur & Dell'Acqua, 2009; Olsson & Poom, 2005). Alvarez & Cavanagh (2004) tested capacity limits for a wide variety of visual items and found that a lower number of complex items can be maintained compared to simple ones. While capacity was around four items for simple colored squares, capacity was far lower, only two items, when the to-be-remembered items were random polygons or shaded 3-D cubes. These results are hard to reconcile with a view that assumes that there is a fixed number of items one can remember.

Research on visual working memory capacity has mostly examined the ways in which capacity is limited. Two competing views have been proposed: the discrete resource view assumes that capacity is limited by a fixed number of objects and the continuous resource view assumes that capacity is limited by an upper limit in the amount of visual information that can be maintained. Over the years, both views have been supported by ample research and a clear consensus on the nature of capacity limits is yet to be reached. One possible way to examine this issue is by finding the exact circumstances under which the effects supporting one view or another arise. For example, currently most research using a typical binary change-detection task has found evidence in favor of a discrete resource view (see for a review: Luck & Vogel, 2013), while research using the continuous report paradigm has favored the continuous resource view (see for a review: Ma et al., 2014). Moreover, studies that found no support for the discrete resource view based on examining visual object complexity has mostly done so by comparing two or more entirely different stimulus classes (e.g., squares versus Chinese characters). It could be that the different capacity estimates between simple and complex object is the result of, for example, a difference in the comparison process at test for squares or Chinese characters, and not actual memorization of these objects. In Chapter 2 we try to address these questions by examining whether capacity is affected when the same visual objects have to be memorized in different levels of complexity.

Visual working memory content

One other way to examine how information is represented in working memory is by trying to deduct what the contents of working memory are. Can we define a ‘unit’ in which information is stored in working memory? For example, Baddeley and Hitch (1974) assumed that visual information was stored as a visual representation in the visuo-spatial sketchpad while verbal information was stored in a verbal code in the phonological loop. Moreover, visual information can be recoded in a verbal code and verbal information can be visualized in a visual representation. Atkinson and Shiffrin (1968) on the other hand assumed that all sensory information was recoded in an amodal code, meaning that the form in which sensory information is stored is independent of its original modality. Cowan (2001) proposed that information is stored in the form of chunks, which assumes that information can be bound in an integrated representation which can in turn be cross-modal (exist of multiple modalities) in nature. Similar to the idea of chunks, in visual working memory research has focused on whether visual information is stored as separate visual features or as integrated visual objects. Visual features are considered to be the basic building blocks of visual objects. To illustrate, a horizontal blue bar is an object which consists of the following visual features: color (blue), shape (height and width), and orientation (90º). Intuitively, it would make sense that we would memorize visual information as integrated objects however research is currently divided on this topic.

Akin to the debate on the limits of visual working memory capacity, the debate on whether we memorize separate features or integrated objects has been instigated by the study of Luck & Vogel (1997). They instructed participants to memorize one or more features (feature load) of one or multiple objects (object load) and found that memory for objects with up to four relevant features was as good as memory for objects with only a single relevant feature. Since visual working memory performance was largely unaffected by the number of features that had to be memorized per object suggested that objects, and not features, are the main unit of visual working memory. This finding has been replicated in multiple studies (e.g., Luria & Vogel, 2011; Vogel et al., 2001; Woodman & Vogel, 2008). In contrast, several studies have found an effect of feature load on visual working memory performance when features that had to memorized came from the same feature dimension (e.g., memorizing two different colors of one object, Olson & Jiang, 2002; Wheeler & Treisman, 2002; Xu, 2002).

For example, Wheeler and Treisman (2002) presented participants with objects consisting of one or multiple (up to six) different colors. They found no difference in performance between memorizing one object with multiple colors or the same number of objects with a single color. When memorized features came from different feature dimensions, however, similar results to Luck and Vogel (1997) were found. Based on these findings, they suggest a framework in which different feature dimensions are memorized in their own domain-specific stores. An additional store can maintain the binding of these features, when the task requires it. Since the features used in a typical change-detection task are selected from different feature dimensions, this framework may explain why object load and not feature load influences working memory performance in these studies.

Recently, evidence has been provided, which shows that feature load can affect visual working memory performance even when the to-be-remembered features are from different feature dimensions (Fougnie, Asplund, & Marois, 2010; Hardman & Cowan, 2015; Oberauer & Eichenberger, 2013; Palmer, Boston, & Moore, 2015; Vergauwe & Cowan, 2015; Wilson, Adamo, Barense, & Ferber, 2012). In one study, Oberauer & Eichenberger (2013) used novel multi-feature objects that could change on six different feature dimensions (shape, color, size, orientation of thick stripes, thickness of thick striped, and the spatial frequency of thin stripes). Using a change detection task, they found that accuracy decreased from one to three features remembered per object and decreased even further from three to six features. This effect was present even when objects were simplified (only 4 features instead of 6), when changes on test were big or small, when response was binary or semi-continuous (8 option forced choice), and when items were presented for short and long time periods. Similarly, in an impressive effort to replicate Luck and Vogel's (1997) original findings, Hardman and Cowan (2015) found an effect of feature load using the exact procedure as the original study. It is important to note that although they found an effect of feature load they also found a big effect of object load on working memory performance. This seems to indicate that both integrated object and separate feature information is maintained in visual working memory (see also, Fougnie et al., 2010).

The discrepancy in the literature regarding the influence of feature load on VWM capacity can possibly be explained by a crucial difference in the stimuli that were used in each study. Authors reporting effects of objects, but not of features, typically only used stimuli consisting of feature combinations that are difficult to process independently of each other (Luck & Vogel, 1997; Luria & Vogel, 2011; Vogel et al., 2001; Woodman &

Vogel, 2008). For example, the stimuli used by Luck & Vogel (1997) were relatively simple objects, consisting of bars of different colors and shapes. Processing the orientation of such a colored bar depends on the shape of that bar, which might encourage automatic feature binding. Because the different features occupy the same spatial area, a form of obligatory binding can occur, minimizing the effects of feature load. Moreover, studies that have found effects of feature load did not manipulate object load (Fougnie et al., 2010; Oberauer & Eichenberger, 2013; Palmer et al., 2015). In Chapter 3 we investigate in which form visual information is stored in working memory by manipulating both object load and feature load in a change detection task with multi-feature items. Moreover, to examine the effect of feature load during memorization we recorded simultaneous EEG (Electroencephalogram) in a second experiment.

Electrophysiology of visual working memory

An important advance in the study of visual working memory capacity research is the discovery of the lateralized event-related potential (ERP) component, known as the Contralateral Delay Activity (CDA, also known as the Contralateral Negative Slow Wave, CNSW, or Sustained Posterior Contralateral Negativity, SPCN). Klaver, Talsma, Wijers, Heinze, and Mulder (1999) found that when presenting an object to a participant in a certain hemifield an ERP slow wave appeared in posterior brain areas contralateral to the presented stimulus. It is important to note here is that this slow wave only appeared when participants were instructed to memorize the presented object and that this wave persisted throughout memorization. They suggested that the increase in ERP negativity reflected an enhancement of the visual information that had to be memorized.

Machizawa and Vogel (2004) expanded on this finding by examining ERP negativity with a bi-lateral version of the change detection task. In this task participants are presented with two different sample areas in each hemifield and are then instructed to only memorize the array in one specified hemifield. This allowed them to examine the moment of memorization in the retention interval and to isolate ERP activity of the attended side from the unattended side. By subtracting the ipsilateral activation from the contralateral activation they created a difference wave. The assumption was that noise in the EEG signal would mostly be present on both the ipsilateral and contralateral side while the memory related activity would only be present on the contralateral side. The subtraction will cancel out the noise signal leaving a 'clean' representation of the memory related activity. Using this method they found that CDA negativity increased linearly with an increase in object load until an individual's capacity limit is reached. Looking at the increase in CDA amplitude between 2 and 4 item arrays, they found a high correlation between the amplitude increase and an individual's calculated capacity. High capacity individuals showed a much larger amplitude increase than low capacity individuals. McCollough, Machizawa, and Vogel (2007) further explored the properties of the CDA and found that the CDA was more negative over recording sites contralateral to the memorized stimulus than over the ipsilateral recording sites, but that this difference became smaller near the end of the retention interval (700-900ms). This smaller difference was due to ipsilateral activity becoming more negative and is thought to represent a later processing of relevant information in the ipsilateral hemisphere. More importantly, they found that CDA negativity increased with object load and not the spatial distribution of the objects, suggesting that the CDA is actively tracking the number of objects in memory and not the overall area remembered. Taken together, these findings show that the CDA is exceptionally suited to examine both the limits and the contents of visual working memory.

Indeed, since then, the CDA has been used to examine a wide variety of topics in visual working memory (see for a review: Luria, Balaban, Awh & Vogel, 2016). Relevant for the current dissertation, only a couple of studies have examined the impact of memorizing individual features on CDA negativity thus far. Similar to the behavioral studies mentioned above, results have been mixed. For example, Woodman and Vogel (2008) found that CDA amplitude was not affected by feature load, although Luria and Vogel (2011) did find an increase in CDA amplitude for feature load. This increase in amplitude was only present in the initial part of the CDA (between 450-600 ms post stimulus presentation) and only when the to-be-remembered features were from the same feature dimension. Wilson et al. (2012), however, found an increase in CDA amplitude driven by feature load in a situation where the to-be-remembered features were from different feature dimensions. Much like the mixed behavioral results mentioned earlier, the discrepancy in results can be the product of using different stimuli in different studies.

In sum, the CDA is a useful tool to examine visual working memory processes during the memorization of visual information. Although the evidence is mixed, some studies did find that the CDA can also reflect effects of feature load (Luria & Vogel, 2011; Wilson et al., 2012). In Chapter 3 we examine CDA negativity for multi-feature objects that are known to elicit a feature load effect in order to gain new insights into the contents of visual working memory.

OUTLINE OF THE CURRENT DISSERTATION

The aim of the current dissertation is to examine the integrative properties of working memory, both within and across modalities. Having established that working memory may be involved in integrating information within a single modality as well as across modalities, we first turn our attention to the integrative properties of working memory within the visual modality.

In Chapter 2, we examine the question to what degree we can control the level of detail with which we can memorize visual stimuli and if precision can be traded in for more capacity to memorize additional objects. This question was addressed using a change detection task in which one or more visual objects had to be memorized. Participants were instructed to memorize these objects at one of three possible levels of detail. Estimates of working memory capacity indicated that memorizing objects at higher levels of detail resulted in a reduction of the number of objects, which could be memorized. In addition, change detection accuracy was affected by both the number of objects memorized as well as the amount of detail memorized per object. The absence of an interaction between the number of objects and the precision of objects, suggests that the number of objects and the amount of detail impacted capacity independently.

In Chapter 3, we examine the effect of feature load on visual working memory capacity, change detection sensitivity, and posterior slow wave ERP activity. Participants memorized arrays of one, or multiple, multi-feature objects and had to report whether one of the objects had changed after a short retention interval. Objects could change on a pre-indicated relevant feature. In the two experiments we conducted, we found that visual working memory capacity was significantly impacted by feature- as well as object load, but found no interactions between these factors, again suggesting that object and feature load modulated working memory capacity independently. Moreover, we observed a discrepancy between lateralized EEG activity that is sensitive to the number of objects memorized and bilateral EEG activity that is more sensitive to the number of features memorized per object.

Following the discussion of integrative properties within the visual modality, we shift our focus to studying these processes across modalities. Although our sensory experience is mostly multisensory in nature, research on working memory representations has focused mainly on examining the senses in isolation. Results from the multisensory processing literature make it clear that the senses interact on a more intimate manner than previously assumed. These interactions raise questions regarding the manner in which multisensory information is maintained in working memory.

In Chapter 4, we examine whether an auditory context can influence the spatial processing and subsequent recall of serially presented visual items in working memory. To do so, we employed a 4-item Sternberg task with visually presented Chinese characters. There were three types of auditory context that could coincide with visual stimulus presentation: a monotone, ascending, or random tone context. We found that processes responsible for the spatial recoding of nonverbal items in serial order working memory can be influenced by an irrelevant auditory context under certain circumstances. It seems that the auditory context needed to facilitate this repositioning has to consist of informative and predictable auditory stimuli.

In Chapter 5, we discuss the current status of research on multisensory processing and the implications of these findings on our theoretical understanding of working memory. We focus on reviewing working memory research conducted from a multisensory perspective, and discuss the relation between working memory, attention, and multisensory processing in the context of the predictive coding framework. We argue that complex representations seem to be formed in working memory, consisting of the integration of several independent representations that can be sensory, and short- or long-term memory activations. Depending on task requirements either just the simple modal representation or the complex high-resolution binding of several features at once will become active.

Finally, in the **general discussion**, we will discuss the implications of our findings on working memory research and current working memory models.

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CHAPTER 2
VISUAL WORKING MEMORY VARIES WITH INCREASED ENCODING DETAIL OF COMPLEX OBJECTS[1]

A major ongoing debate in visual working memory research concerns the question whether the number of objects or the amount of total information that can be stored limits visual working memory capacity. The object-limited view assumes that a fixed number of objects can be maintained in an all or nothing approach. The information-limited view, on the other hand, assumes that a varying number of objects can be maintained dependent on the precision with which these objects are encoded. Here, we examine whether the visual complexity of an object can affect the number of objects stored in working memory. Specifically, we wanted to examine whether capacity was affected when the same objects had to be memorized with varying levels of detail. Participants memorized arrays of one or more complex objects and had to report whether one of the objects had changed on a relevant dimension after a short retention interval. Change relevance was determined by the task instruction received at the beginning of a block. We found that visual working memory capacity was significantly impacted by the amount of detail that had to be memorized per object. In addition, change detection accuracy was affected by both the number of objects memorized as well as the amount of detail memorized per object. Moreover, results suggest that the precision of encoding is under voluntary control to a certain degree. These findings are discussed in light of the above-mentioned views on the emergence of capacity limits.

[1] Quak, M., Bigler, A., & Talsma, D. (in preperation). Visual working memory varies with increased encoding detail of complex objects.

INTRODUCTION

Visual short-term memory, also known as visual working memory, is our ability to temporarily maintain a representation of visual items in memory without the physical presence of these items. For example, when playing a game of cards with friends we are able to maintain the specific cards we currently have in our hands without actively looking at them. This ability enables us to watch the moves of our friends and plan our own turn while they play their cards. When we hold more and more cards in our hands it becomes more difficult to keep these cards in memory. The number of items we can store in working memory has been estimated to be around 3 to 4 items (Cowan, 2001; Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001). The capacity of our working memory is subject to individual differences (Vogel & Machizawa, 2004) and is highly correlated with a wide variety of cognitive functions, such as general intelligence, academic career, and reading comprehension (e.g., Alloway and Alloway, 2010; Conway, Cowan, Bunting, Therriault, & Minkoff, 2002; Daneman & Carpenter, 1980). It is therefore very important to understand how these capacity limits come about. There are currently two competing ideas that can explain capacity limits. The first idea is that capacity is object-limited, that is, we can store a fixed number of objects in memory, regardless of the information density per object (Luck & Vogel, 1997, Cowan, 2001, Zhang & Luck, 2008). The second idea, in contrast, is that capacity is information-limited. More specifically, this idea states that capacity is limited by a fixed amount of visual information, regardless of whether this information is distributed among multiple objects or not (Alvarez & Cavanagh. 2004; Bays & Husain, 2008; Wilken & Ma, 2004). Over the years support has been found for both models and is the reason why this is a major point of discussion in the visual working memory literature.

Visual working memory capacity has mostly been investigated by using the so-called change detection task: Participants are presented with a set of objects, which they have to subsequently memorize. Then participants are presented with another set of objects and they have to indicate whether a change has occurred in this new set of objects, compared to the initially presented set. This task is fairly simple and assumes that as long as the capacity limits of the working memory system are not reached, change-detection performance will be good. When this limit is reached, for example by increasing the size of the set of objects presented, detection performance will deteriorate.

Using this task, Luck and Vogel (1997) were the first to show that participants could maintain, on average, up to four objects. When the number of objects was increased beyond four, performance dropped systematically with each added object. Moreover, changing the amount of visual information that had to be memorized per object (e.g., memorize the color of an object or memorize the shape, color, and rotation of an object) had no impact on working memory performance. This led to the view that visual information is memorized in the form of bound objects and that memory capacity is limited by a fixed number of objects you can memorize (Cowan, 2001; Luck & Vogel, 1997; see for a review: Luck & Vogel, 2013). This view has been supported by a large number of studies (Anderson, Vogel, & Awh, 2011; Aw, Barton, & Vogel, 2007; Ikkai, McChollough, & Vogel, 2010; Scolari, Vogel, & Awh, 2008; Vogel & Machizawa, 2004; Vogel, Woodman, & Luck, 2001; Zhang & Luck, 2008). Most of these studies have used the detection of relatively large changes, for example, a red square changing into a blue square instead of a red square changing into a slightly different shade of red square. A notable limitation of this approach is that it makes it difficult to draw inferences about the precision with which each object is maintained.

A pure object-limited view of working memory capacity assumes that objects in working memory are always stored in their entirety in an all or nothing approach. This position has been challenged, however, in a series of studies that examine the precision of object representations in working memory. These studies have reported evidence for the view that the amount of information that is memorized per object can in fact vary and that this in turn can affect the number of objects that can be memorized (Bays, Catalao, & Husain, 2009; Bays, Gorgoraptis, Wee, Marshall, & Hussain, 2011; Bays & Husain, 2008; Fougnie, Cormiea, Kanabar, & Alvarez, 2016; Wilken & Ma, 2004;). The task used in these studies was a modified version of the change detection task. Here, instead of issuing a binary response (i.e. by stating that a change has occurred or not), participants are required to reproduce a specific aspect (e.g., color) of one or more of the objects during test. For example, by examining the discrepancy between the actual color of the object and the one reproduced from the participants' memory, an estimate of the precision of that item's representation in working memory can be obtained. It has been shown this discrepancy increases as a function of the number of objects that have be memorized (Bays et al., 2009; Bays et al., 2011; Bays & Husain, 2008; Fougnie et al., 2016; Wilken & Ma, 2004). Thus, it appears that there is a trade-off between the number of objects and the precision with which these objects can be stored. Moreover, this trade-off appears to be under strategic control (Fougnie et al., 2016). In other words, participants can choose to memorize more objects in a less precise way, or the other way around. These studies show strong support for the view that capacity is information and not object-limited: There is no fixed number of objects we can store but with each added object in memory the representation of these objects becomes less and less precise.

Over the years evidence for both views has been accumulating with a clear winner far out of reach. For example, studies that have used a binary change detection task in which a participants' expectancy of change magnitude was manipulated gave mixed results. A number of studies have shown that the visual complexity of the memorized items in itself can influence working memory capacity (e.g., Alvarez & Cavanagh, 2004; Diamantopoulou, Poom, Klaver, & Talsma, 2011; Eng, Chen, & Jiang, 2005; Luria, Sessa, Gotler, Jolicoeur & Dell'Acqua, 2009; Olsson & Poom, 2005). For example, Alvarez & Cavanagh (2004) tested capacity limits for a wide variety of visual items and found that a lower number of complex items can be maintained compared to simple ones. While capacity was around four items for simple colored squares, capacity was far lower, only two items, when the to-be-remembered items were random polygons or shaded 3-D cubes. Studies examining object complexity have mostly done this by comparing capacity for one group of visual items (e.g., simple colored squares) to capacity for a different group of visual items (e.g., random polygons). Although these studies did point to a trade-off between capacity and stimulus complexity, they did not address the question to what degree the level of detail in memorization is under voluntary control. Results addressing the latter question using a binary change detection task are mixed. Some studies did find evidence that participants could strategically change the precision with which they memorized objects (Gao, Yin, Xu, Shui, & Shen, 2010; Machizawa, Goh, and Driver, 2012) while others did not (Murray, Nobre, Astle, & Stokes, 2012; He, Zhang, Li, & Guo, 2015; Ye, Zhang, Liu, Li, & Liu, 2014). Given these discrepancies, it remains to be determined whether participants can indeed voluntarily choose to memorize objects in a more or less precise fashion.

The aim of the current study was to do so by examining whether the visual complexity of an object can affect the number of objects stored in working memory. Specifically, we wanted to examine whether capacity was affected when the same objects had to be memorized with varying levels of detail. We did so by varying the amount of detail participants were instructed to memorize. This was accomplished by creating novel stimuli that could be varied and memorized at three levels of detail. Each visual stimulus consisted of six squares in a random configuration within a 3 by 4 square grid. Of these six squares, three random squares would always be white and the remaining three squares would have the same random color. The distribution of white and colored squares created a unique checkerboard like pattern. These visual objects were used in a typical change-detection task with a varying set size of 1 to 4 objects. Participants were instructed at the beginning of each block to memorize either: 1) the shape, 2) the shape and the color, or 3) the shape, the color, and the spatial distribution of white and colored squares of each object (or pattern). We specifically analyzed the capacity estimates (Cowan's K) per level of detail and accuracy measures to examine the interaction between the level of detail and the number of objects that had to be memorized. If capacity is limited by a fixed number of objects regardless of visual complexity, we would expect no difference in capacity measures (Cowan's K) between the different levels of detail. Moreover, we would expect accuracy to only be affected by the number of objects that had to be memorized and not by the level of detail with which these objects had to be memorized. If, on the other hand, capacity is limited by a fixed amount of visual information, regardless of how this is divided over objects, we would expect that capacity measures (Cowan's K) do change as a function of the amount of detail that had to be memorized. Also, we would expect that both the number of objects as well as the amount of detail memorized affects accuracy.

Additionally, to incentivize participants to process the entire object, regardless of the amount of detail they were instructed to memorize, all separate dimensions of an object could change on test. Traditionally in a change-detection test when parts of an object are designated as 'relevant' only the relevant part will change or not (cf. Luck & Vogel, 1997). In the current study all dimensions of an object could change between the sample and test array. For example, when participants were instructed to memorize the shape of the object if a change would occur not only the shape could change but also the color or pattern could change. If a change occurred only one of the possible dimensions would change per trial. Participants were instructed to only respond 'change' when a relevant dimension changed (e.g., the shape changed when instructed to memorize shape) and 'no change' when an irrelevant aspect changed (e.g., the color, pattern, or nothing changed). One study by Awh et al. (2007) has shown that sample-test similarity and not necessarily visual complexity can account for differences in capacity found between simple and complex objects.

METHOD

Participants

Twenty-three undergraduate students (age 18 – 25) participated in this study in exchange for course credit. All participants gave informed consent and reported having normal color vision and normal or corrected-to-normal eyesight.

Materials

The experiment was programmed in OpenSesame using the PsychoPy back-end (Mathôt, Schreij, & Theeuwes, 2012; Peirce, 2007). All memory arrays that were used in the change detection task (see below) consisted of one to four multi-feature objects. Objects were presented on a gray background in a 12° by 8° area surrounding fixation. Objects were randomly assigned to a location in one of the four quadrants of the larger area. Objects could vary along three different dimensions; shape (the configuration of six squares within a 3x4 square grid), color (three of the squares were given the same color randomly selected from the colors available), and pattern (the configuration of the three colored and three white squares within the shape). Each object was created online and consisted of a random configuration of six squares within a 3x4 grid of visual angle 3.2° by 2.8°. Of the six squares in an object, three were given the same color randomly selected from a fixed color set (red "#FF0000", orange "#FF6A00", yellow "#FFD800", light green "#B6FF00", green "#4CFF00", blue "#00FFFF", light blue "#0094FF", dark blue "#0026FF", purple "#B200FF", violet "#E100DC" and pink "#E1006E"). The other squares were white.

Colored and white squares where randomly placed within the shape configuration to create a spatial distribution. For every trial objects were randomly generated from the feature options available.

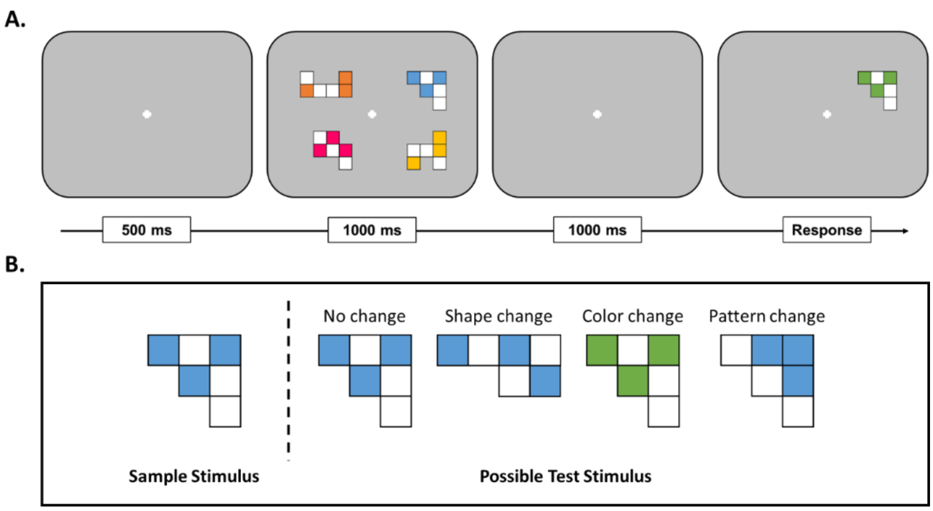

Figure 1. Example change-detection trial sequence and possible stimulus change. (A) Each trial started with an initial fixation period for 500 ms. A memory array with one or multiple objects was presented for 1000 ms followed by a blank retention interval for 1000ms. The test array containing one of the objects from the memory array was shown until response. Participants indicated whether a change had occurred on the instructed dimension(s). (B) There were 4 possible changes between sample and test: no change, a shape change, color change, or pattern change.

Procedure

Participants were seated behind a personal computer approximately 60 centimeters in front of the monitor. The task started with general instructions explaining the task. Before each block participants were instructed to memorize the shape, the shape and color, or the shape, color, and pattern of the objects. Each block started with sixteen practice trials. Each trial started with a fixation cross in the middle of the screen for 500 ms. A memory array was presented for 1000 ms, which was followed by a 1000 ms retention interval in which no stimuli were presented. After the retention interval the response display was presented until participants made their response (see Figure 1A for an overview of the trial sequence). During the response display one of the earlier presented objects would be repeated with one of four possible changes; a shape change, color change, pattern change, or no-change (see Figure 1B for an example of possible dimension changes). The memorization condition (memorize shape, shape and color, and shape, color, and pattern) determined whether a specific change was relevant (e.g., a shape or color change in the memorize shape and color condition) or irrelevant (e.g., a color, pattern, or no-change in the memorize shape condition; see Table 1 for an overview of memorization conditions and the distribution of relevant and irrelevant changes). Responses were made on a keyboard by pressing either the ‘z’ or ‘m’ key to report a relevant or irrelevant change, respectively. The stimulus response mapping switched halfway through the experiment and was counterbalanced between participants. After response a white or red fixation dot was shown for 500 ms to indicate correct or incorrect answers respectively.

The three different memorization conditions were administered in separate blocks in a random order for each participant. There were a total of 192 trials in every memorization condition of which half of the trials were change trials.

Table 1 *Overview of memorization conditions, types of change, and distribution over trials*

Memorize	Type of change	# of trials	Change relevancy
Shape	Shape	96	Relevant
	Color	32	Irrelevant
	Pattern	32	
	No change	32	
Shape and color	Shape	48	Relevant
	Color	48	
	Pattern	48	Irrelevant
	No change	48	
All	Shape	32	Relevant
	Color	32	
	Pattern	32	
	No change	96	Irrelevant

Analyses

To investigate the overall impact of memorizing more detail on working memory capacity we calculated Cowan's *K.* Cowan's *K* was calculated by (proportion hits – proportion false alarms) * set size (Cowan, 2001) for each participant for each memorization condition. Maximum *K* values were used as the capacity estimate per participant per memorization condition. In cases where Mauchly's test indicated that the assumption of sphericity had been violated degrees of freedom were Greenhouse-Geisser corrected.

RESULTS

Cowan's K

Mean *K* for all conditions are shown in Figure 2. A one-way repeated-measures ANOVA on Detail (shape, shape and color, or shape, color and pattern) shows that *K* decreased significantly when more detail had to be memorized per object, $F(2, 44) = 5.080$, $p < .010$, $\eta_p^2 = .188$. Within subject contrasts revealed that *K* was significantly higher when memorizing shape compared to shape, color, and pattern $F(1, 22) = 10.322$, $p < .004$, $\eta_p^2 = .319$. Pairwise comparisons revealed no significant difference between memorizing shape, and memorizing shape and color ($p = .241$) and between memorizing color and shape and memorizing shape, color and pattern ($p = .703$).

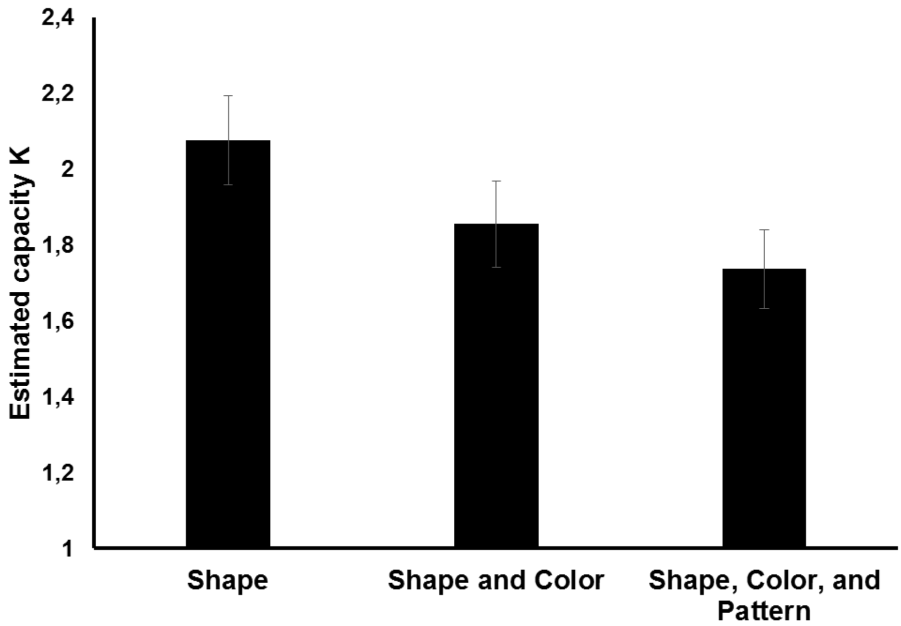

Figure 2. The effect of amount of detail (shape, shape and color, shape, color, and pattern) memorized per object on Cowan's *K.* Error bars represent standard errors of the mean.

Accuracy

The average accuracy for all conditions is shown in Figure 3. Differences in accuracy were analyzed in a 3 (Detail: shape, shape and color, or shape, color, and pattern) x 4 (Set size: 1, 2, 3, or 4) x 2 (Change: relevant, or irrelevant) repeated measures ANOVA. A significant main effect of Set size was observed, $F(3, 66) = 122.911$, $p < .000$, $\eta_p^2 = .848$. Accuracy decreased with an increase in Set size from 1 to 4 objects. Pairwise comparisons revealed that change detection accuracy decreased significantly when more objects needed to be remembered from 1 to 2 objects ($p < .000$), from 2 to 3 objects ($p < .000$), and from 3 to 4 objects (p = .002). There was also a significant main effect of Detail, $F(2, 44) = 7.332$, $p < .002$, $\eta_p^2 = .250$. Accuracy decreased when more detail of an object was memorized, from memorizing shape to shape and color (p= .003), and from shape to shape, color, and pattern (p =.035) but not from shape and color to shape, color, and pattern (p=.585). No significant effect of Change was observed, average accuracy was the same for relevant change and irrelevant change trials. The interaction between Detail and Change was significant (Figure 3B), $F(2, 44) = 5.733$, $p < .006$, $\eta_p^2 = .207$. Contrasts revealed that accuracy for irrelevant change trials was significantly lower compared to relevant change trials but only when memorizing the shape and color of objects, $F(1, 22) = 12.320$, $p < .002$, $\eta_p^2 = .359$. There was no difference in relevant change and irrelevant change trials when memorizing either the shape, or the shape, color, and pattern of an object, $F(1, 22) < 1$. We also observed a significant interaction between Set size and Change, $F(3, 66) = 3.707$, $p < .035$, $\eta_p^2 = .144$. Visual inspection suggests a difference between relevant change and irrelevant change trials, but only when memorizing four objects, where accuracy is lower on irrelevant change trials. The interaction between Detail and Set size was not significant (Figure 3A), $F(6, 132) = 1.507$, $p < .181$, $\eta_p^2 = .064$. The 3-way interaction between Detail, Set size, and Change was also not significant, $F(6, 132) = 1.162$, $p < .331$, $\eta_p^2 = .050$.

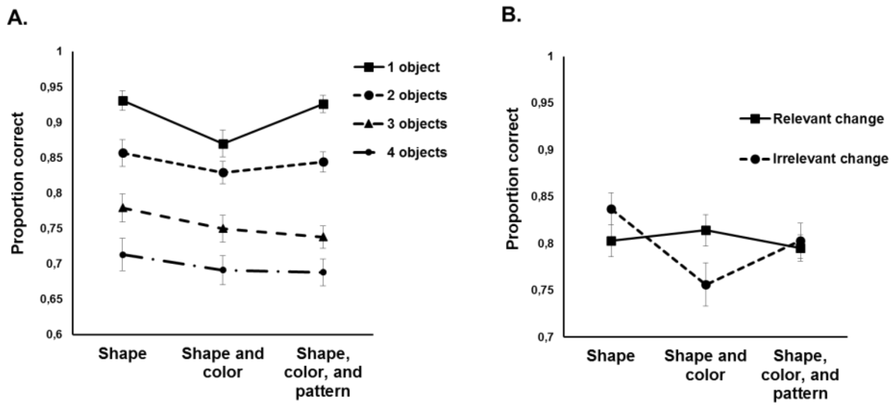

Figure 3. Behavioral results: (A) The effect of amount of Detail (shape, shape and color, shape, color, and pattern) memorized per object, and set size (1 to 4) on proportion correct. (B) The effect of amount of detail (shape, shape and color, shape, color, and pattern) memorized per object, and Change (relevant or irrelevant) on proportion correct. Error bars represent standard errors of the mean.

To further examine the interactions of the different changes on change detection performance we conducted an additional analysis of memorization detail and the type of change. Because there was an unequal amount of trials for each change in each condition we randomly selected an equal number of trials for each condition. This left 32 trials per condition for the 2-way analysis. Average accuracy for Detail and Change are shown in Figure 4. There was a significant main effect of Detail, $F(2, 44) = 5.826$, $p <.006$, $\eta_p^2 = .209$. Pairwise comparisons revealed that accuracy was significantly higher when memorizing shape only, compared to memorizing shape and color ($p < .015$), or shape, color, and pattern ($p < .032$). There was no difference between the shape and color, and the shape, color and pattern condition ($p < 1$). A significant main effect of Change was observed, $F(33, 66) = 30.943$, $p <.000$, $\eta_p^2 = .584$. Pairwise comparisons revealed that change detection accuracy was higher when color changed compared to a shape change ($p < .000$), a detail change ($p < .000$), and no-change ($p < .002$). Change detection accuracy was worse when the pattern changed compared to a color change ($p < .000$) or no-change ($p < .000$), and showed a trend towards significance compared to a shape change ($p < .086$). There was no difference in accuracy between a shape change and no-change ($p < .375$). There was a significant interaction between Detail and Change, $F(6, 132) = 13.278$, $p <.000$, $\eta_p^2 = .376$. When looking at a shape change compared to no-change for all three memorization conditions, the distribution is somewhat the same across conditions, accuracy for shape change and no-change conditions are better when only memorizing shape compared to memorizing shape and color, and shape, color and pattern. When looking at the color and detail change conditions an interesting pattern emerges. In the memorize shape condition, a color change is irrelevant and does not affect memory performance. When memorizing shape and color, a color change becomes a relevant change and accuracy for detecting a color change is much higher compared to a shape change or no-change. Color change detection improves even more when shape, color, and pattern had to be memorized. For detail the opposite seems to occur, when memorizing shape only, just like a color change a detail change is irrelevant and does not affect change detection performance. However, when memorizing shape and color, an irrelevant detail change affects performance drastically and performance drops even more when memorizing shape, color, and detail, where detail is a relevant change.

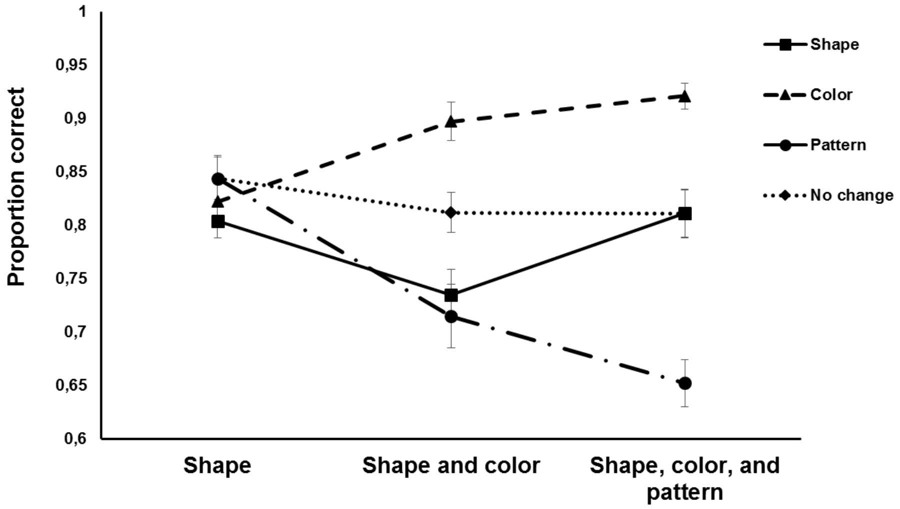

Figure 4. The effect of amount of detail (shape, shape and color, shape, color, and pattern) memorized per object, and test change (shape, color, pattern, and no change) on proportion correct. Error bars represent standard errors of the mean.

DISCUSSION

The current study aimed to examine whether the visual complexity of an object can affect the number of objects stored in working memory. Specifically, we wanted to examine whether capacity was affected when the same objects had to be memorized with varying levels of detail. Participants memorized arrays of one or more complex objects and had to report whether one of the objects had changed on a relevant dimension after a short retention interval. Change relevancy was determined by the task instruction received at the beginning of a block. Participants were instructed to memorize the shape, the shape and color, or the shape, color, and pattern of the same objects. The main finding of the current study was that visual working memory capacity was significantly impacted by the amount of detail that had to be memorized per object. In addition, change detection accuracy was affected by both the number of objects memorized as well as the amount of detail memorized per object. There was no significant interaction between the two factors, suggesting both the number of objects and the amount of detail impacted capacity independently.

The results of the current study are in agreement with studies that have shown that the same objects can be memorized with varying precision and that this precision, in turn, can impact the number of objects that can be memorized (Bays et al., 2009; Bays et al., 2011; Bays & Husain, 2008; Fougnie et al., 2016; Wilken & Ma, 2004). Our results also agree with studies that have shown that the visual complexity of an item can impact capacity (Alvarez & Cavanagh, 2004; Diamantopoulou et al., 2011; Eng et al., 2005; Luria et al., 2009; Olsson & Poom, 2005), but extend the latter findings, by showing that this trade-off between level-of-detail and number of items can be strategically controlled. The novel finding in our study was that participants were instructed to memorize these objects in differing levels of detail, and that it was this instruction that caused the above-described differences in capacity estimates. Thus, our results suggest that participants were able to control the precision with which they memorized the same objects in a top-down manner (cf., Gao et al., 2010; Fougnie et al., 2016; Machizawa et al., 2012).

Our results are clearly incompatible with a pure object-limited account of visual working memory. The object-limited account states that capacity is limited by a fixed number of bound objects that can be stored in visual working memory, because all information of an object would have been bound and stored together regardless of the relevancy of that information (Cowan, 2001; Luck & Vogel, 1997). As such, the object-limited account would predict that the same number of objects can be retained in memory in each and every condition. Because of this obligatory binding of information, a pure object-limited account would predict that participants are unable to strategically control the precision with which the same items are stored. The results of the current study do not support this view.

It is important to note here that this pure version of the object-limited account has made way for an updated version, known as the slot + averaging model (Zhang & Luck, 2008). Employing the same methods as Wilken and Ma (2004), i.e. by requiring participants to reproduce one specific feature of a memorized object, Zhang and Luck (2008) found evidence that was compatible with a modified version of the object-limited account. More specifically, they did find a fixed upper limit of three objects that could be memorized simultaneously; a finding that is consistent with the object-limited account. Extending this finding, however, Zhang and Luck (2008) also found that the precision of the representation in memory decreased as a function of the number of items retained memory. This decrease in reproduction precision is incompatible with the object-limited account, but does fit with an information-limited account. To explain these findings Zhang and Luck concluded that capacity is limited by a fixed amount of discrete slots but that when only one item is memorized, copies of the single item are made and stored in the remaining slots, thereby increasing the precision of the representation of that item. Our data are compatible with such a view and based on the data we cannot fully differentiate between the information-limited explanation and the slot + averaging explanation.

Despite the impact of increased detail memorization on capacity we also still found a major impact of the number of objects stored on change detection accuracy. This finding suggests that both the number of objects and the amount of detail per object can limit visual working memory. Furthermore, the lack of an interaction between the two might indicate that they both impose a limit on working memory capacity in their own way. Indeed, over the years, some research groups have suggested a hybrid view of capacity limits, where both the number of objects and their precision affect capacity independently (e.g., Alvaraz & Cavanagh, 2004; Xu & Chun, 2006). For example, based on the results that capacity for simple objects was much higher than capacity for complex objects, Alvarez and Cavanagh (2004) concluded that capacity is limited by an upper bound in the number of objects that can be stored but that within that upper bound capacity can be flexibly allocated depending on item complexity.

Although the results of the current study are in agreement with recent studies, we should be careful with making any strong claims based on this study. One problem in the current study was the nature of the stimuli used in the change detection task. The different dimensions of the stimuli were interrelated, meaning that a change on one dimension would also change another dimension. For example, when the shape of an object changed, the spatial distribution of colored and white squares also changed. Moreover, it has been shown that changing the spatial location of colors (as when the spatial distribution changed in current study) can severely impact change detection performance (e.g., Olivers & Schreij, 2014), even when the location information is task irrelevant (Jiang, Olson, & Chun, 2000; Kondo & Saiki, 2012; Treisman & Zhang, 2006). This could explain some of the findings in our additional analyses that looked at the amount of detail memorized and the type of change that occurred. When participants memorized shape and color we saw an improvement on color change detection and a decline when the pattern changed compared to the memorize shape only condition. We speculate that the difference on the color change is explained by the increased relevancy of the color change detection in the memorize shape and color condition compared to the shape only condition. The decline of performance on the pattern change can be explained by an increase in uncertainty on whether a color change has occurred. When the pattern changed so did the location of the colored squares, when participants are instructed to indicate whether the color has changed, the change in a colors' location can cause uncertainty and with that more errors (cf., Jiang et al., 2000; Kondo & Saiki, 2012; Treisman & Zhang, 2006). More importantly, the proposed increased uncertainty on test could explain the main effect in the current study in the same way as the increase in detail can. Increased uncertainty on test and not the increase in detail during encoding could have been responsible for the decline in working memory performance. It is possible that the irrelevant feature changes on test and the uncertainty it brings is what drives our main effect instead of an increase in memorized detail. How irrelevant feature changes can affect change detection performance is an interesting line for future research. Currently, studies that have examined this have found mixed results. For example, Woodman, Vogel, and Luck (2012) found no evidence that change detection performance was affected by irrelevant size or location changes. Others have shown that although irrelevant features can be encoded automatically in a change detection task, this only affected change detection performance when relevant memory load was low (Xu, 2010), or when the retention interval was short (<500 ms, Logie, Brockmole, & Jaswal, 2010).

Lastly, it could be argued that we did not really manipulate the amount of detail participants had to memorize per object (or the precision), but instead manipulated the amount of visual features that had to be memorized per object. While precision and the number of visual features memorized per object are closely related, as in the amount of visual features can affect the precision with which objects are memorized (e.g., Fougnie, Asplund, and Marois, 2010), they are not the same. How the number of visual features affect working memory capacity will be discussed in Chapter 3 of this thesis.

The current study sought to address the question to what degree we can control the level of detail with which we can memorize visual stimuli and if precision can be traded in for more capacity to memorize additional objects. This question was addressed using a change detection task in which one or more visual stimuli had to be memorized. Participants were instructed to memorize these stimuli at one of three possible levels of detail. Estimates of working memory capacity indicated that memorizing stimuli at higher levels of detail resulted in a reduction of the number of items which could be memorized.

These results are compatible with information-limited models of working memory, which state that the total amount of information that has to be memorized is the limiting factor in working memory, regardless of how this information is distributed across individual objects. One novel finding in the current study is that the trade-off between level of detail and number of objects is to a certain degree under voluntary control.

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CHAPTER 3
BILATERAL BUT NOT LATERALIZED POSTERIOR SLOW WAVE ACTIVITY REFLECTS FEATURE LOAD IN VISUAL WORKING MEMORY [1]

A major ongoing debate in visual working memory research concerns the question whether visual working memory capacity is determined only by the number of objects that have to be memorized, or by the number of relevant features contained within these memorized objects. Here, we examine the effect of feature load on visual working memory capacity, change detection sensitivity, and posterior slow wave event-related brain potential (ERP) activity during memory retention using a change detection task with multi-feature objects. Working memory capacity and sensitivity decreased significantly as a function of both the number of objects and the number of features memorized per object. Contralateral Delay Activity (CDA) was strongly sensitive to the number of objects, but not to the number of features. Additional analyses of both ipsilateral and contralateral brain activity, however, revealed a pattern that also reflected feature processing. We conclude that objects as well as features contribute to limitations in visual working memory capacity and that bilateral and lateralized slow wave activity might reflect two separate systems that underlie feature and object processing

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[1] Quak, M., Langford, Z.D., London, R.E., & Talsma, D. (under revision). Bilateral but not lateralized posterior slow wave activity reflects feature load in visual working memory

INTRODUCTION

Humans are equipped with the ability to maintain information in an active state beyond the immediate sensory experience. This cognitive ability – commonly referred to as ‘working memory’ – allows us to maintain various types of information (e.g., verbal, visual) and is a key factor across many daily activities. For example, in the absence of visual working memory, imagine how tremendously effortful it would be to ride a bicycle in busy traffic. Indeed, we are constantly processing incoming visual information, selecting and holding on to relevant parts of the stream, and integrating them into a coherent visual scene according to our current goals. A major ongoing issue in the domain of visual working memory concerns the question of how we encode, maintain and recall visual information: Do we store individual features of an item in memory, fully integrated items, or a combination of both? In other words: Is it possible to define what Fougnie, Asplund, and Marois (2010) refer to as a “unit” of working memory that we can use to describe in which form information is stored?

The literature is currently divided as to whether information is maintained as integrated objects, or whether the individual features of objects are stored independently. One way to address this issue is to measure visual working memory capacity. A task that is often used for measuring capacity is the change-detection paradigm. In this paradigm, participants are rapidly presented with an array of items that needs to be memorized, followed by a short retention interval. After the retention interval participants are presented with a test array, which can either be identical to the memory array, or differ from it on one specific feature of a single item (for example, in an array of colored squares, one of the squares may have changed color). On each trial, participants report whether a change has occurred between the memory and test array, and the accuracy on this task can be used to estimate capacity.

Using this task, several studies have reported that visual working memory capacity is determined solely by the number of objects that have to be memorized (object load), regardless of the number of features that constitute these objects (feature load; Luck & Vogel, 1997; Luria & Vogel, 2011; Vogel, Woodman, & Luck, 2001; Woodman & Vogel, 2008). For example, Luck & Vogel (1997) provided evidence that memory for objects with up to four relevant features was as good as memory for objects with only a single relevant feature. The fact that the number of features to be memorized did not seem to influence visual working memory capacity suggested that objects, but not features, are the units of visual working memory. In contrast, several other studies (Olson & Jiang, 2002; Wheeler & Treisman, 2002; Xu, 2002) did find effects of features on working memory capacity when features were from the same feature dimension, and others (Fougnie et al., 2010; Hardman & Cowan, 2015; Oberauer & Eichenberger, 2013; Palmer, Boston, & Moore, 2015; Vergauwe & Cowan, 2015; Wilson, Adamo, Barense, & Ferber, 2012) observed similar effects of features across feature dimensions. This would suggest that objects are not stored in working memory in a completely integrated manner. For example, Oberauer & Eichenberger (2013) used novel multi-feature objects, and found that change detection accuracy decreased from one to three features remembered per object and decreased even further from three to six features. The question whether information is maintained as integrated objects, or whether the individual features of objects are stored independently has therefore not been resolved on the basis of these studies.

An important advance in the study of visual working memory was the discovery of a lateralized event-related potential (ERP) component, known as the Contralateral Delay Activity (CDA). Klaver, Talsma, Wijers, Heinze, and Mulder (1999) found a clear contralateral slow-wave ERP during memorization of one polygon during the memorization and retention interval of a change detection task. Vogel and Machizawa (2004) have expanded on this finding by showing that CDA negativity increased linearly with an increase in object-load until an individual’s capacity limit is reached. Since then, the CDA has been used to examine the limitations of visual working memory (see for a review: Luria, Balaban, Awh & Vogel, 2016). Thus far, only a couple of studies have examined the impact of memorizing individual features on CDA negativity, and similarly to behavioral studies, with varying results. One study by Woodman and Vogel (2008) found no change in CDA amplitude for feature load. By contrast, Luria and Vogel (2010) found an increase in CDA amplitude for feature load, but only in the initial part of the CDA (between 450-600 ms post stimulus presentation) and only when the to-be-remembered features were from the same feature dimension. Wilson et al. (2012) found an increase in CDA negativity for conjunction stimuli compared to single feature stimuli in a situation where the to-be-remembered features were from different feature dimensions.

This discrepancy in the literature regarding the influence of feature load on VWM capacity that is apparent both in purely behavioral as well as psychophysiological studies could possibly be explained by a crucial difference in the low-level stimulus features that were employed in each study. Authors reporting effects of objects, but not of features, typically only used stimuli consisting of feature combinations that are difficult to process independently of each other (Luck & Vogel, 1997; Luria & Vogel, 2011; Vogel et al., 2001;

Woodman & Vogel, 2008). For example, Luck & Vogel (1997) used relatively simple objects, consisting of bars of different colors and shapes. Processing the orientation of such a colored bar is contingent upon the shape of that bar, thus promoting automatic feature binding. Because the different features occupy the same spatial area, a form of obligatory binding can occur, minimizing the effects of feature load. Such automatic binding could be avoided by using more complex stimuli, in which multiple features can be more or less independently manipulated and processed. Indeed, studies employing this stimulus type have typically reported an effect of feature load. These studies, however, did typically not manipulate the object load (Fougnie et al., 2010; Oberauer & Eichenberger, 2013; Palmer et al., 2015).

In order to fully understand the dynamics between feature and object processing, the independent manipulation of both object-load and feature-load would be required. For example, Hardman & Cowan (2015) found that both the number of objects and the number of features determine working memory capacity. It should be pointed out, however, that the type of stimuli that Hardman and Cowan (2015) used, might lead to an underestimation of the effect of feature load because features occupied the same spatial location. Oberauer and Eichenberger's (2013), stimuli might be better suited for the independent manipulation of features and objects, because they comprise multiple features with their own spatial boundary within an object, allowing for a better separation of single features.

The goal of the current study was to determine in which form visual information is stored in working memory. We used a novel approach to investigate whether the capacity of working memory depends on object load and/or feature load. In addition, we investigated the neural correlates of object and feature processing by using the above-mentioned CDA ERP component (Klaver et al., 1999; Vogel & Machizawa, 2004). We used a set of stimuli based on those of Oberhauer and Eichenberger (2013) which allowed us to manipulate object and feature load independently (see Figure 1). All objects were colored rectangles with differing heights and widths, and surrounded by black borders. Inside the rectangular objects, three black lines were drawn that could change in thickness and orientation. In the two experiments presented here we used a change detection task (see Figure 1). First, a memory array with a varying number of multi-feature objects was presented (In Experiment 2, the memory array was preceded by a cue that indicated which of the two hemifields needed to be remembered) followed by a short retention interval. After the retention interval, a test item was presented on the location of one of the objects from the memory array and participants indicated whether the object had changed on one of the relevant features. Participants were informed at the beginning of each block what the relevant feature(s) were, and that a change could only occur for those feature(s). We specifically sought to measure working memory performance as a function of the number of objects and the features per object that had to be remembered by calculating sensitivity (*d`*) and capacity (Cowan's *K*) measures. *D*-prime is an often-used measure of sensitivity that is independent of personal response biases towards change or no-change answers in a change detection task. Cowan's *K* is a measure that estimates a participant's visual working memory capacity.

In experiment 2, we focused on the neural correlates of the interaction between feature and object load, by investigating the CDA component. We examined both object load and feature load and their respective effects on CDA negativity in posterior brain areas. We expected that feature load would affect visual working memory capacity for objects (Cowan’s *K*) and that both objects and features would affect change detection sensitivity (*d*`). For Experiment 2 we expected that the increase in memory load by both objects and features would be reflected in CDA negativity. To foreshadow, our results show that working memory capacity is influenced by both object load and feature load, and that objects are therefore not stored in a completely integrated manner.

METHOD EXPERIMENT I

Participants

Twelve undergraduate students (mean age 18 years, 11 female) participated in Experiment 1, in exchange for course credit. All participants gave informed consent and reported having normal color vision and normal or corrected-to-normal eyesight. One participant was excluded from further analyses because of performance levels that were below chance level.

Material

The experiment was programmed in OpenSesame using the PsychoPy back-end (Mathôt, Schreij, & Theeuwes, 2012; Peirce, 2007). All memory arrays used in the change detection task (see below) consisted of one to four rectangular objects, and were based on the stimuli used by Oberauer and Eichenberger (2013). Objects were presented on a gray background in an 11.56° by 7.68° area surrounding fixation. Objects were randomly assigned to a location in one of the four quadrants of the larger area. All objects were colored rectangles with a thin black outline and (three) thick black lines inside the rectangle (see Figure 1). Objects could vary along four different feature dimensions: shape, color, the thickness of the black lines within each object, and the orientation of the black lines within each object. Height and width were randomly determined per object, but all objects had the same surface area, on average 2.64° by 2.64° in visual angle. For every trial objects were randomly composed from the feature options available. Table 1 gives an overview of the dimensions of the features used and the change that could occur between sample and test array.

Table 1 *Feature dimensions used in Experiment 1 and 2, with the possible feature values of each object and the amount of change that could occur on a change trial*

Feature dimensions	Possible feature values	Feature change
Shape width (in pixels)	70, 80, 90, 100, 110, 120, 130, 140	+40 or -40 pixels
Color (in hexadecimal)	Red (#FF0000), Orange (#FF6A00), Yellow (#FFD800), Light green (#B6FF00), Green (#4CFF00), Cyan (#00FFFF), Light blue (#0094FF), Blue (#0026FF), Violet (#B200FF), Magenta (#E100DC), Pink (#E1006E)	+4 or -4 steps in color
Line orientation (in degrees)	11, 29, 47, 65, 83, 101, 119, 137	+72 or -72 degrees in Experiment 1, +18 or -18 in Experiment 2
Line thickness (in pixels)	7, 12, 17, 22, 27, 32, 37, 42	+20 or -20 pixels

Note. Shape height was determined by dividing 10000 by the width

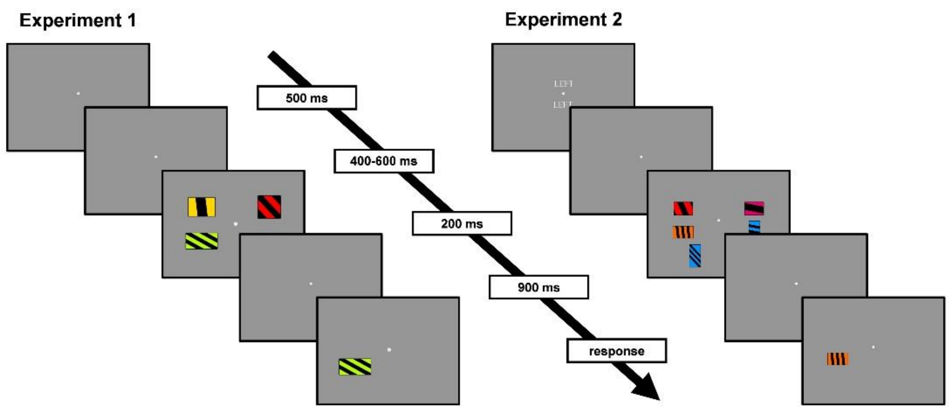

Figure 1. Example change-detection trial sequence of Experiment 1 and Experiment 2. Each trial started with an initial fixation period (with location cue in Experiment 2) for 500 ms followed by random fixation period of 400, 500, or 600 ms. A memory array with one or multiple multi-feature objects presented for 200 ms preceded a blank retention interval for 900ms. The test array containing one of the multi-feature items from the memory array was shown until response. Participants indicated whether a change had occurred on the relevant feature dimension(s).

Procedure

Participants were seated behind a personal computer approximately 60 centimeters in front of the monitor. The task started with general instructions explaining the change detection task. Before each block participants were instructed what the relevant feature(s) for that block would be (shape, color, orientation, thickness, shape and color, orientation and thickness, or all) and received eight practice trials before each block. Each trial started with a fixation dot in the middle of the screen for 900, 1000, or 1100 ms, randomly selected on each trial. Then the memory array was presented for 200 ms followed by a 900 ms retention interval in which no stimuli were presented. After the retention interval the response display was presented until participants made their response (see Figure 1A for an overview of the trial sequence in Experiment 1). Responses were made on a keyboard by pressing either the ‘z’ or ‘m’ key to report a change or no-change, respectively. The stimulus response mapping switched halfway through the experiment and was counterbalanced between participants. After response a red or white fixation dot was shown for 120 ms to indicate incorrect or correct answers respectively.

The three different experimental conditions (single-feature, two-features, and four-features) were administered in separate blocks in a random order for each participant. There were a total of seven different experimental blocks: Four single-feature blocks, where one of the four features was the relevant feature: color, shape, thickness, or orientation; two two-feature blocks, where two of the features were relevant: color and shape or thickness and orientation; and one four-feature block, where all four features were relevant. In the single-, and two-feature-change conditions only the relevant (to-be-remembered) features could change in the test display. In the four-feature-change condition all features could change and every feature change occurred the same number of times within a block. There were a total of 64 trials in every experimental condition (number of objects: one, two, three, and four; number of features: one, two, or four) of which half of the trials were change trials.

Analyses

To explore the interaction between object load and feature load we calculated *d′* for each number of objects and features per participant. Hit and false alarm rates were used to calculate *d′* values (cf. Stanislaw and Todorov, 1999). Scores of 0 were replaced by 0.5/total and scores of 1 were replaced by (total-0.5)/total where *total* is the total number of trials in that condition (Macmillan & Creelman, 2005).

To investigate the overall impact of feature load on working memory capacity we calculated Cowan's *K*. Cowan's *K* was calculated by (proportion hits – proportion false alarms) * set size (Cowan, 2001) for each participant for each condition. Maximum *K* values were used as the capacity estimate per participant per feature condition.

In cases where Mauchly's test indicated that the assumption of sphericity had been violated degrees of freedom were Greenhouse-Geisser corrected.

RESULTS EXPERIMENT I

D-prime

Average *d′* values for all conditions are shown in Figure 2A. Differences in the *d'* values were analyzed in a 3 (Feature load: 1, 2, or 3) x 4 (Object load: 1, 2, 3, or 4) repeated measures ANOVA. A significant main effect of Object load was observed, $F(3, 30) = 108.141$, $p < .000$, $\eta_p^2 = .915$. D-prime decreased with increasing memory load from 1 to 4 objects. Pairwise comparisons revealed that change detection accuracy decreased significantly when more objects needed to be remembered from 1 to 2 objects ($p < .000$), from 2 to 3 objects ($p < .001$), and from 3 to 4 objects ($p = .003$). There was also a significant main effect of Feature load, $F(2, 20) = 13.016$, $p < .000$, $\eta_p^2 = .566$. D-prime decreased from 1 to 2 features remembered ($p = .006$), and 1 to 4 features ($p = .007$) but not from 2 to 4 features ($p=1$). Not only object load but also feature load had a significant impact on VWM capacity. The interaction between Object load and Feature load was not significant. A 3 (Feature Load) x 4 (Object load) repeated measures ANOVA on β showed no significant main effect on Object load, ($p = .136$) or Feature load ($p = .625$), and no significant interaction between the two ($p = .573$). This indicates that participants did not adopt a different response pattern across the different conditions.

Cowan's K

Estimated capacity (*K*) values per feature load are shown in Figure 2B. A one-way repeated-measures ANOVA on Feature load (1, 2, or 4) shows that *K* decreased significantly when more than one feature needed to be memorized, $F(2, 20) = 19.979$, $p < .001$, $\eta_p^2 = .666$. Pairwise comparisons reveal that *K* did not decrease further between the 2 and 4 feature conditions.

To be sure that the effect of Feature load was not due to the different feature dimensions used in the experiment, we also calculated *K* for Feature load and the feature dimension that was relevant (see Figure 2C). A 3 (Feature load: 1, 2, or 4) x 4 (Feature dimension: shape, color, orientation, or thickness) repeated-measures ANOVA on maximum *K* showed a significant effect of Feature load, $F(2, 20) = 17.921$, $p < .001$, $\eta_p^2 = .642$. *K* decreased when more features were required to be memorized. *K* did not decrease beyond 2 features. Pairwise comparisons revealed a significant difference between 1 and 2 features ($p = .001$), and 1 and 4 features ($p = .006$), but not between 2 and 4 features ($p = .330$). There was a significant main effect for Feature dimension, $F(3, 30) = 8.249$, $p < .001$, $\eta_p^2 = .452$. Contrast analyses revealed that *K* was significantly higher for color compared to orientation ($p = .002$), and significantly lower for orientation compared to color ($p = .002$), and thickness ($p = .014$). No significant difference was observed between shape and color ($p = .239$), shape and thickness ($p = 1$), shape and orientation ($p = .708$), and color and thickness ($p = .587$). There was no significant interaction between Feature load and Feature dimension. Capacity was affected equally for all features by the number of features that needed to be remembered.

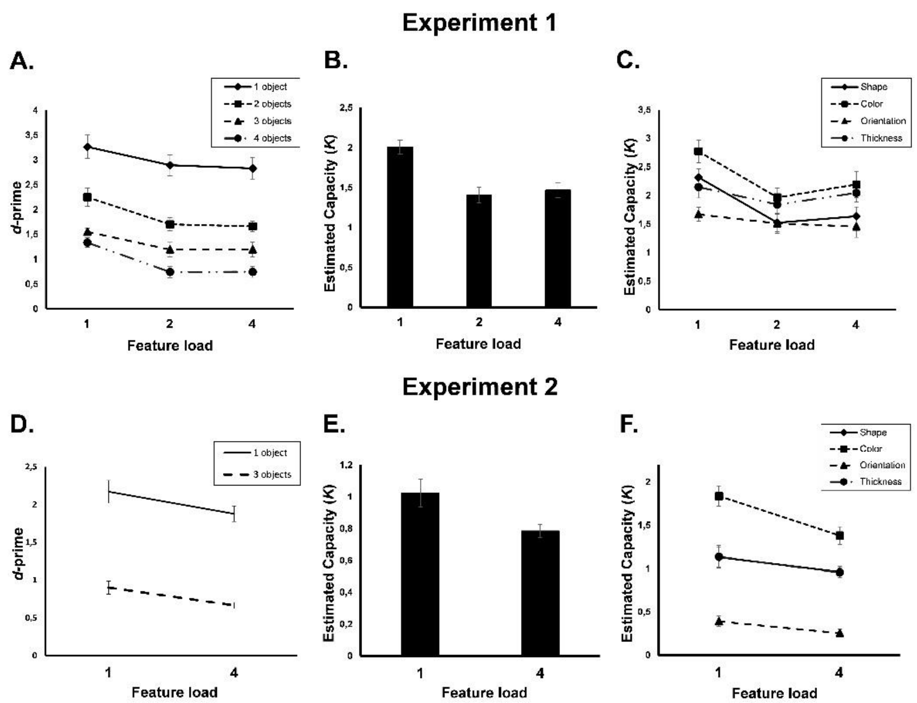

Figure 2. Behavioral results as represented by *d*-prime and Cowan's *K* of Experiment 1 and Experiment 2. The results for Experiment 1: (A) the effect of feature load (1, 2 or 4 features) on average *d*-prime per object load (1, 2, 3, or 4); (B) the effect of feature load on Cowan's *K*; (C) The effect of feature load on Cowan's *K* per feature dimension (shape, color, line orientation, and line thickness).The results for Experiment2: (D) the effect of feature load (1 or 4 features) on average *d*-prime per object load (1 or 3); (E) the effect of feature load on Cowan's *K*; (F) The effect of feature load on Cowan's *K* per feature dimension. Error bars represent standard errors of the mean.

DISCUSSION EXPERIMENT I

In Experiment 1 we sought to investigate how object load and feature load affect visual working memory capacity. We measured change detection performance while varying object load and feature load independently. We calculated *d*` to measure change detection sensitivity and Cowan's *K* to look at the impact of feature load on visual working memory capacity.

Change detection performance, as measured by Cowan's *K* and *d*`, dropped significantly when more objects had to be memorized. Crucially, change detection performance was also affected by feature load, supporting the idea that the basic unit of visual working memory cannot be defined by objects alone, and that features indeed play a role as well. Feature load had a significant impact on visual working memory capacity as defined by Cowan's *K*. This effect was not due to differences in memorization difficulty of the different feature dimensions: Even though we observed differences in capacity for the different feature dimensions (with the biggest difference between color and orientation), increasing the number of features that had to be memorized affected capacity equally across all feature dimensions. These results are consistent with earlier findings that indicate that feature load affects the number of objects we can successfully store in working memory (Fougnie, et al., 2010; Hardman & Cowan, 2014; Oberauer & Eichenberger, 2013; Palmer, et al., 2015; Vergrauwe & Cowan, 2015). While both the number of objects and the number of features affected change detection, they did not interact. It seems that object load and feature load influence memory independently.

Interestingly, our estimates of Cowan's *K* and *d*` did not decrease beyond a feature load of two. This might be due to the relatively small feature load in the current experiment. Indeed, Oberhauer and Eichenberger (2013) did find a further decrease in change detection performance beyond a feature load of two. In their study, participants had to memorize either one, three or six features per object. Alternatively, the lack of an effect of feature load beyond memorizing two features might suggest that after an initial cost, memorizing more features does not affect working memory further. This is in line with a notion by Alvarez & Cavanagh (2004), who suggested that when memorizing an object, a core set of features is automatically included in the memory trace. Memory performance will then only be affected when features outside of this core set need to be memorized. In the current study one or multiple features could have been part of the core feature set and thus overestimate the actual number of features memorized in the four-feature condition. Similarly, it could be argued that the specific features used in this experiment allow for a separation of an object in two parts, a colored square and an oriented line stimulus, and that the found cost of features is because participants memorized more parts (or objects) instead of more features. However, this seems unlikely because it would assume that adding a relevant feature of the same part (e.g., adding color when memorizing shape) would not show a decrease in performance, which is not what visual inspection of the data (Figure 2c) suggests.

Our results support the idea that the basic unit of visual working memory is defined both by objects as well as features (e.g., Fougnie et al., 2010; Hardman & Cowan, 2014) and the effect of feature load cannot be accounted for by a pure object based view (e.g., Luck & Vogel, 1997; Luria & Vogel, 2011; Vogel et al., 2001; Woodman & Vogel, 2008). We believe the contradictory findings in the literature may be caused by differences in the type of multi-feature objects used in those studies. Some types of object might encourage binding due to the different feature dimensions within one object occupying the same spatial area, whereas other objects might make binding difficult due to the different features being from separate dimensions as well as at separate spatial locations. While the type of objects used in the experiments can explain some of the contradictions in the literature we do not think it is the only cause of these contradictions. For example, it fails to explain the contradictory results of Luck and Vogel (1997) and Hardman and Cowan (2014) who used exactly the same materials and methods in their respective studies.

It can still be argued that the effect of features in current and previous studies (Fougnie, et al., 2010; Hardman & Cowan, 2014; Oberauer & Eichenberger, 2013; Vergrauwe & Cowan, 2015) is due to a process other than memorization of the stimuli. For example, the number of features might affect performance during retrieval or response (Awh, Barton, & Vogel, 2007; Busch & Herrmann, 2003). To examine the effect of feature load during memorization we recorded simultaneous EEG in Experiment 2.We were specifically interested in the effect of feature load on activity over posterior brain areas reflected by the CDA waveform. We expected that CDA negativity would increase with object load as well as feature load. Also, we expected that feature load would affect visual working memory capacity for objects (Cowan's *K*) and that both object load and feature load would affect change detection sensitivity (*d*`).

METHOD EXPERIMENT II

Participants

Sixteen undergraduate students (mean age 27 years, 10 female, all right handed) participated in Experiment 2, in exchange for payment. All participants gave informed consent and reported having normal color vision and normal, or corrected-to-normal eyesight. Two participants were excluded from further analyses because over 50% of epochs were removed after artifact rejection.

Material

With the exception of the following parameters the same material was used as in Experiment 1. All memory arrays consisted of one or three rectangular objects presented in each hemifield. All objects were presented on a gray background in a 15° by 15° area. There were four possible locations in each hemifield surrounding fixation. Locations of objects were randomly selected on each trial from the available options. Objects used were identical to the objects used in Experiment 1. For every trial, objects were randomly created from the options available. Table 1 gives an overview of the dimensions of the used features and the change that could occur between sample and test array.

Procedure

With the exception of the following parameters the same procedure was used as in Experiment 1. Participants were seated behind a personal computer with their chin in a chinrest 60 centimeters in front of the monitor. The general trial sequence was the same as Experiment 1 except that the first fixation screen was replaced with a cue (the word left or right presented above and below a fixation dot; see Figure 1B for an overview of the trial sequence in Experiment 2).

The two different conditions (single-feature and four-features) were administered in separate blocks in a random order for each participant. There were a total of five different experimental blocks: Four single-feature blocks, where one of the four features was the relevant feature: color, shape, thickness, or orientation; and one four-feature block, where all four features were relevant. In the single-feature change conditions only the relevant (to-be-remembered) features could change in the test display. In the four-feature-change condition all features could change and every feature change occurred the same number of times within a block. There were a total of 320 trials in every experiment condition (number of objects: one or three; number of features: one or four) of which half of the trials were change trials.

Electrophysiological recordings and preprocessing

EEG data were collected using a Biosemi ActiveTwo system (Biosemi, Amsterdam, Netherlands) with 64 Ag–AgCl scalp electrodes positioned according to the standard international 10–20 system. Additional electrodes were attached to the left and right mastoids to be used as a reference. Electrodes at the outer canthi of both eyes and directly above and below the right eye were used for acquiring a horizontal and vertical electrooculogram (EOG). Signals were recorded with a sampling rate of 512 Hz. During preprocessing, a band-pass filter with a high-pass cutoff of 0.01 and a low-pass cutoff of 30 Hz was applied after which data was resampled to 256 Hz. Data was re-referenced offline to the average of the left and right mastoid. Eye blinks were corrected using independent component analysis (ICA). Bad channels were interpolated by calculating the average activity of surrounding electrodes. The data were epoched from −200 ms to 1100 ms, time-locked to the onset of the memory array. Simple voltage threshold (larger than 75 μV) automatic artifact rejection together with visual inspection was used to remove trials with extreme values.

EEG Analysis

For each condition separately, average waveforms were calculated over trials and participants. Contralateral waveforms were generated by averaging activation on left stimulus presentation and right hemisphere electrodes and activation on right stimulus presentation and left hemisphere electrodes. Ipsilateral waveforms were generated by averaging activation on left stimulus presentation and left hemisphere electrodes and right presentation on right hemisphere electrodes. CDA difference waves were calculated by subtracting ipsilateral activation from contralateral activation. CDA amplitude was calculated by averaging the mean amplitude in the range of 200 to 1100 ms post stimulus-presentation. Trials containing artifacts or incorrect behavioral responses were excluded from the averaging procedure. On average 15% of total trials (range 2.7% – 38.7%) were removed per participant. The number of removed trials were evenly distributed across conditions.

RESULTS EXPERIMENT II

D-prime

D` values where calculated using the same method as used in Experiment 1. Average *d′* values for all conditions are shown in Figure 2D. A 2 (Object load: 1, or 3) x 2 (Feature load: 1, or 4) repeated-measures ANOVA. There was a significant main effect of Object load, $F(1, 13) = 240.093$, $p < .001$, $\eta p^2 = .949$. When participants memorized more objects their change-detection performance decreased compared to when they memorized a single object. A significant main effect of Feature load, $F(1, 13) = 17.241$, $p = .001$, $\eta p^2 = .570$, indicated that memorizing more features per object significantly decreased change-detection performance. The interaction between objects and features was not significant. A 2 (Feature load: 1, or 4) x 2 (Object load: 1, 3) repeated measures ANOVA on β showed a significant main effect of Object load, $F(1, 13) = 30.895$, $p < .001$, $\eta p^2 = .704$. β was significantly higher for 1 object compared to 3 objects. We observed no significant main effect of Feature load ($p = .201$). There was a significant interaction between Object load and Feature load, $F(1, 13) = 4.734$, $p = .049$, $\eta p^2 = .267$. The difference between 1 and 4 features memorized per object was bigger when participants memorized 1 object compared to 3 objects.

Cowan's K

Estimated capacity (*K*) values were calculated for each condition and participant (see Figure 2E). A one-way repeated-measures ANOVA (Feature load: 1, or 4) showed a significant effect of Feature load, $F(1, 13) = 13.610$, $p =.003$, $\eta p^2 =.511$. Capacity decreased when more features needed to be memorized per object. We also calculated maximum *K* for Feature load and the feature dimension that was relevant (see Figure 2F). A 2 (Feature load: 1, or 4) x

4 (Feature dimension: shape, color, orientation, or thickness) repeated-measures ANOVA on maximum K showed a significant main effect of number of Feature load, $F(1,13) = 14.351$, $p = .002$, $\eta p^2 = .525$. There was furthermore a significant main effect of Feature dimension, $F(3, 39) = 84.811$, $p < .001$, $\eta p^2 = .867$. Capacity was affected by the type of feature that needed to be remembered. Capacity for color was significantly higher compared to shape ($p = .001$), orientation ($p < .001$), and thickness ($p = .001$). Capacity for orientation was significantly lower compared to color ($p < .001$), shape ($p < .001$), and or thickness ($p < .001$). There was no difference in capacity between shape and thickness. The interaction between Feature load and Feature dimension was not significant, $F(3, 39) = 2.567$, $p = .068$, $\eta p^2 = .165$.

Electrophysiology

Contralateral and Ipsilateral wave forms averaged across electrode sites P7 and P8, PO3 and PO4, and PO7 and PO8 are shown in Figure 3A. Average amplitude of the CDA waveform and the CDA difference wave are shown in Figure 3B. A 2 (Object load: 1, or 3) x 2 (Feature load: 1, or 4) repeated measures ANOVA on CDA mean amplitude revealed a significant main effect of Object load, $F(1, 13) = 28.367$, $p < .001$, $\eta p^2 = .686$. The CDA amplitude was significantly more negative when participants memorized 3 objects compared to when they memorized 1 object. All other main and interaction effects were not significant (p's > .385). Surprisingly, despite the clear effects of Feature load in behavior, we did not find any effect of Feature load on CDA amplitude. Because of this discrepancy we conducted the following additional analysis.

A 2 (Object load: 1, 2) x 2 (Feature load: 1, 4) x 2 (Lateralization: contralateral, ipsilateral) repeated measures ANOVA on mean amplitude showed the expected significant main effect of Lateralization, $F(1, 13) = 18.575$, $p = .001$,

ηp^2 = .588. Mean amplitude was more negative contralateral than ipsilateral. More interesting is that we found a significant main effect of Feature load, $F(1, 13) = 7.032$, $p = .020$, $\eta p^2 = .351$. Mean amplitude was more negative when memorizing one feature per object compared to four features per object. Coincidentally, we found no significant main effect of Object load, $F(1, 13) = 3.549$, $p = .082$, $\eta p^2 = .214$. Mean amplitude was the same when memorizing 1 or 3 objects. However, the interaction between Object load and Lateralization was significant, $F(1, 13) = 28.370$, $p < .001$, $\eta p^2 = .686$. Amplitude negativity increased significantly between 1 and 3 objects but only contralateral and not ipsilateral. Moreover, the interaction between Feature load and Lateralization was not significant, $F(1, 13) < 1$, $p = .443$, $\eta p^2 = .044$. Other main and interaction effects not mentioned were not significant (p's $> .235$). To confirm the topographical distribution of contralateral and ipsilateral activation, average ipsilateral and contralateral amplitudes across the scalp for each condition are plotted in Figure 3C.

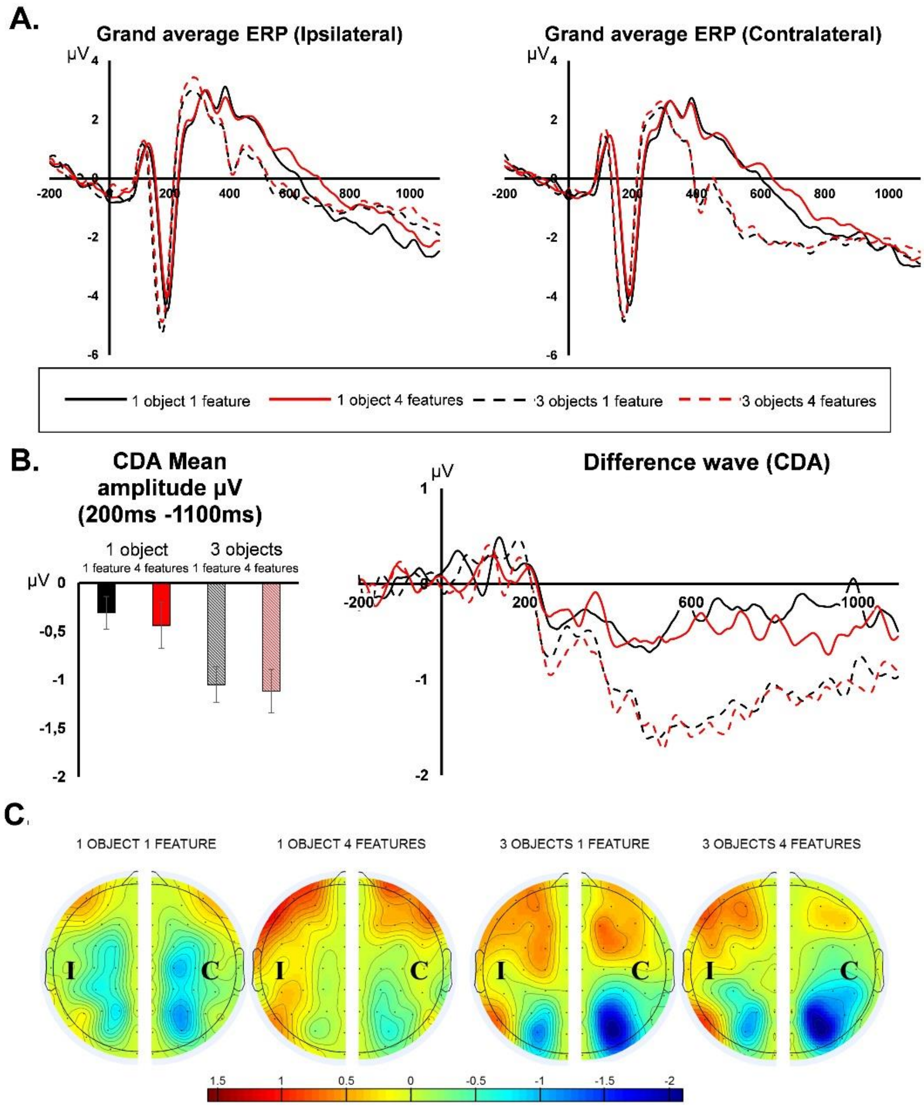

Figure 3. ERP results for Experiment 2. (A) Grand average wave forms of mean amplitude in microvolt (μV) over time (ms) for ipsilateral and contralateral activity averaged across electrode sites P7 and P8, PO3 and PO4, and PO7 and PO8. Solid lines represent object load 1 and dotted lines object load 3, black lines represent feature load 1 and blue lines feature load 4. (B) CDA mean amplitude

between 200 and 1100 ms post stimulus presentation per condition and the CDA difference wave averaged over electrode sites P7 and P8, PO3 and PO4, PO7 and PO8. (C) scalp topographies show mean amplitude ipsilateral and contralateral between 200 and 1100 ms for all conditions.

DISCUSSION EXPERIMENT II

In Experiment 2 we sought to investigate the neural activity related to feature and object processing in visual working memory. To do so, we used a change-detection task similar to that employed in Experiment 1, but now using a lateralized presentation of the stimuli and using two levels of stimulus load and feature load. The main finding of this experiment was that the CDA component was strongly sensitive to object load, but not to feature load. However, additional analyses of both ipsilateral and contralateral brain activity revealed a more intricate pattern of results that also reflected feature processing, showing that feature load does have an impact on brain activity during VWM maintenance.

At a behavioral level, change detection performance dropped significantly as a function of both feature and object load. Both capacity estimates (Cowan's *K*) and sensitivity (*d*-prime) decreased with increasing feature and object loads. As was the case in Experiment 1 we found no evidence for an interaction between object and feature load. These findings are consistent with other studies that showed effects of feature load on working memory performance (Hardman & Cowan, 2014; Oberauer & Eichenberger, 2013; Palmer, et al., 2015; Vergauwe & Cowan, 2015).

As mentioned above, CDA amplitude is largely unaffected by feature load. This result is consistent with findings by Woodman and Vogel (2008) who also found no change in CDA amplitude for feature load. In contrast to the current study however, Woodman and Vogel (2008) did not find an effect of feature load in their behavioral data. While the difference in behavioral results between the current study and that of Woodman and Vogel (2008) could be explained by the difference in multi-feature objects used across these experiments, it is more difficult to explain the CDA results in these terms. To the best of our knowledge the current study is the first to show this discrepancy between the behavioral effects and CDA amplitude. The implications of this discrepancy will be discussed below.

GENERAL DISCUSSION

In this study we aimed to examine the effect of feature and object load on visual working memory capacity. Specifically we sought to examine the interplay between these two factors, both at the behavioral as well as at the electrophysiological level. Participants memorized arrays of one, or multiple, multi-feature objects and had to report whether one of the objects had changed after a short retention interval. Objects could change on a pre-indicated relevant feature. In the two experiments we conducted, we found that visual working memory capacity was significantly impacted by feature- as well as object load, but found no interactions between these factors, suggesting that object and feature load modulated working memory capacity independently. In Experiment 2, CDA amplitude increased as a function of object load, but not of feature load. When we subsequently analyzed the ipsilateral and contralateral slow wave activity independently, we did find an effect of feature load: The mean ERP amplitude during retention was less negative when memorizing four features compared to memorizing one feature.

The current study replicates the basic finding that feature load can affect visual working memory capacity (Cowan, Blume, & Saults, 2013; Hardman & Cowan, 2014; Oberauer & Eichenberger, 2013; Olson & Jiang, 2002; Palmer, et al, 2015; Vergauwe & Cowan, 2015; Wheeler & Treisman, 2002; Xu, 2002). More importantly, this is the first study that shows that the CDA component is only affected by object load despite a clear impact of feature load on behavioral performance. Instead, effects of feature load were reflected in a bilateral increase in negativity. These findings support the idea that the CDA component itself is only sensitive to object load (cf., Woodman & Vogel, 2008).

When looking at contralateral and ipsilateral posterior slow-waves in the same electrodes used in the computation of the CDA we do find an effect of feature load. A higher feature load was represented by a more positive slow-wave compared to a lower feature load. Similar effects of feature load on posterior slow waves were found by Kursawe and Zimmer (2015). In their study participants memorized colored polygons, which could change in color, shape, or both. Because stimulus presentation was unilateral and not bilateral (which is required for the CDA) the authors looked at posterior slow-wave activity. They found a more positive going slow-wave for the shape-color conjunction condition compared to the shape only condition. It is interesting that, but as of yet unknown, why an increase in feature load results in a more positive wave-form, but an increase in object load generally results in a more negative wave-form. Future research is needed to answer this question.

In the current study, the effect of feature load on posterior slow-wave amplitude seems to be an effect that occurs on both the ipsilateral and contralateral side. This might indicate that some form of feature processing is occurring on the ipsilateral side. We are not the first to show that some visual processing might occur on the ipsilateral side in working memory. For example, Arend and Zimmer (2011) examined whether delay activity ipsilateral to the relevant items represents processing of relevant or irrelevant items. Activity contralateral to the relevant items increased in negativity with an increase of relevant item set-size. When the relevant set-size was 1 item, contralateral activity was more positive when there was 1 irrelevant item presented compared to 2 or 3 irrelevant items. Activity ipsilateral to the relevant items did not increase with an increase in relevant items. However, when the relevant set-size was 1, ipsilateral negativity increased as the number of irrelevant items increased from 1 to 2, and from 2 to 3. These findings indicate that ipsilateral activity might reflect stimulus processing in some situations. Moreover, some researchers (e.g., McCollough, Machizawa, & Vogel, 2007) report a decrease in CDA amplitude due to an increase in ipsilateral negativity in the latter part of the retention interval. This increase ipsilateral negativity is thought to represent a later processing of relevant information in the ipsilateral hemisphere.

While there is no apparent effect of object load on bilateral delay activity, there is an interaction between object load and lateralization. The difference in amplitude between memorizing one or three objects was much larger on the contralateral side compared to the ipsilateral side. The interaction between object load and lateralization and the lack of interaction between feature load and lateralization might explain why we find an effect in the CDA for object load but not feature load. CDA computation is based on a difference in amplitude between contralateral and ipsilateral sides. As is the case in the current study, the effect of object load on delay activity is often bigger on the contralateral side compared to the ipsilateral side. When computing the CDA these lateralized differences will become more apparent while bilateral effects, the effect of feature load in current study, will be abated.

The discrepancy between the CDA results, and both the bilateral ERP results and behavioral findings indicates that at least two independent mechanisms are contributing to the retention of information in visual working memory: a lateralized object-based mechanism and a bilateral feature-based mechanism. A similar conclusion was drawn by Xu and Chun (2006) who found two separate systems in visual working memory in an extensive functional magnetic resonance imaging (fMRI) study. They found that activity in the inferior intraparietal sulcus was limited by a fixed number of objects at different spatial locations, whereas activity in the superior intraparietal sulcus and lateral occipital complex was related to stimulus complexity and the overall amount of visual information that was encoded.

In line with the results of Xu and Chun (2006), Fougnie et al. (2010) suggested a model that can explain how objects and features contribute independently to the limitations of visual working memory. This model predicts that the number of objects affects the precision of memory and the general storage capacity, whereas the number features only affects memory precision. When object load increases, the probability that objects are encoded in working memory and the precision with which they are encoded decreases. Increasing feature load will only affect the precision of information that is represented in the encoded objects.

The notion that multiple mechanisms are involved in retaining information in working memory is compatible with studies showing that effects of feature load can occur under specific circumstances. Wheeler and Treisman

(2002) suggested a framework in which different feature types are memorized in their own domain-specific stores. An additional store can maintain the binding of these features, when the task requires it. This framework may thus explain why object load and not feature load influences working memory performance in a typical change-detection task. The multi-feature objects typically used in these studies consist of features from distinct dimensions (Luck & Vogel, 1997; Vogel et al., 2001; Woodman & Vogel, 2008). According to Wheeler and Treisman (2002), these features can be retained in their own specific store and therefore do not affect working memory performance. Several studies (Olson & Jiang, 2002; Wheeler & Treisman, 2002; Xu, 2002) indeed support this idea by showing that feature load does affect working memory capacity, but only when those features are from the same feature dimension (e.g., color-color conjunctions). When features are from different feature dimensions (e.g., shape and color, or color and orientation) object memory is typically not affected. It is important to note, that the idea that effects of feature load are only found when the memorized features share a single dimension seems to be at odds with our results and those of the aforementioned studies that also show effects of feature load across dimensions (Fougnie, e al., 2010; Cowan, et al., 2013; Hardman & Cowan, 2014; Oberauer & Eichenberger, 2013; Palmer, et al., 2015; Vergauwe & Cowan, 2015).

It appears that visual working memory is more flexible than a whole-object account would suggest. Two recent studies have found that task instructions can change the strategy with which participants memorize visual information (Vergauwe & Cowan, 2015; Fougnie, Cormica, Kanabar, & Alvarez, 2016). Using a novel reaction time task Vergauwe and Cowan (2015) show that objects and features can both be used depending on the task requirements. When binding between features was not encouraged, retrieving feature information was more difficult, but when feature binding was encouraged retrieving object information was more difficult. This suggests that the unit of working memory is not fixed and can be flexibly adapted to task requirements.

Taken together, the results of the current study indicate that both objects and features contribute to limitations in visual working memory capacity. The discrepancy between lateralized EEG activity that is sensitive to the number of objects memorized and the bilateral EEG activity that is more sensitive to the number of features memorized per object, suggests that two separate systems might underlie the processing of object and feature information in visual working memory retention.

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CHAPTER 4
WORKING MEMORY SCAFFOLDING: DOES AUDITORY CONTEXT FACILITATE WORKING MEMORY MAINTENANCE. INTEGRATION OF SENSES, SPACE AND ORDER IN WORKING MEMORY [1]

An ongoing question in working memory research is how serial order information is encoded, represented, and retrieved. A dominant feature of models explaining serial order processing is that to-be-remembered items are bound to specific position markers. One idea is that these position markers are spatial in nature based on experiments that show a clear relationship between serial order memory and spatial processing on a horizontal axis. In the current experiment we examine whether an auditory context can influence the spatial processing and subsequent recall of serially presented visual items in working memory. Using a cross-modal Sternberg task we found that spatial processing of nonverbal items only occurred when items in a sequence were presented together with a specific auditory context that was both predictable and informative. Spatial processing did not improve visual item recall.

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[1] Quak, M., Abrahamse, E., van Dijck, J.P., & Talsma, D. (in preperation). Working memory scaffolding: Does auditory context facilitate working memory maintenance. Integration of senses, space and order in working memory

INTRODUCTION

Memorizing serial order is one of the key functions of working memory. When asked to memorize a telephone number it is not only important to recall the actual numbers but also the order in which they have to be dialed. How serial order is encoded, represented, and maintained in working memory is still an ongoing question, which spawned multiple models (see for a review: Marshuetz, 2005). One idea is that serial order is maintained by placing the numbers on an internal spatial template in working memory (Abrahamse, van Dijck, & Fias, 2016; Abrahamse, van Dijck, Majerus, & Fias, 2014). In the current study we wished to examine whether a cross-modal context could influence the internal spatial processing of items in memory and if this would facilitate serial order working memory.

One of the ways with which serial order item memory has been investigated is by using the Sternberg task (Sternberg, 1966). In this task, participants are instructed to maintain a series of items that are sequentially presented in the middle of the screen. After a retention period, a target item is presented, and the task is to determine as fast and accurate as possible whether this item belonged to the presented memory sequence or not. Responses are given on one of two predefined response buttons. This paradigm was originally conceived as a method to investigate scanning in verbal working memory. It is based on the assumption that if response selection requires information maintained in working memory, response delays can inform us on the underlying processes when retrieving this information.

In the original study, participants were also instructed to memorize the order in which the items were presented and after the initial target response they were asked to reproduce this order. Since the inclusion of the order instruction and task had no effect on the initial item verification task, it was later dropped from the procedure (see for a review, Sternberg, 1976). The task is now considered to investigate how item information (and not order) is retrieved from working memory (Majerus et al., 2006, 2010). Since Sternberg performance is independent from the instruction to encode order information (e.g., Sternberg, 1975), this might suggest that order information is automatically encoded. Indeed, Guida, Leroux, Lavielle-Guida, & Noël (2015) observed spontaneous serial order coding in a Sternberg task without the explicit instruction to memorize serial order. Therefore the Sternberg task is ideally suited to explore spontaneous serial order representations.

One of the dominant features of models explaining serial order maintenance is that of position marking (see for a review: Hurlstone, Hitch, & Baddeley, 2013). It suggests that to-be-remembered items are bound to specific long-term memory markers and that serial order recall is achieved by retrieving these bindings. Little is known about the cognitive nature of position markers. In a recent proposal, Abrahamse, et al. (2014) assume that the position markers used to memorize serial order items are grounded in an internal and spatial coordinate system. Specifically, items are assumed to be bound to specific coordinates of an internal space (cf. working memory; see for reviews: Abrahamse et al., 2014, 2016). Spatial attention is used to search through the serial order representation in working memory and select items for retrieval. There is growing evidence for this proposal.

For example, using a modified Sternberg task van Dijck and Fias (2011) found that retrieving items presented early in a sequence elicited faster left handed responses whereas items presented later in a sequence elicited faster right handed responses. Participants were presented with sequences of 5 items (numbers, or fruits and vegetables) with a self-paced presentation time. During the retention interval, all possible items were presented twice in random order and participants were asked to do a categorization task (by parity, odd or even, for numbers, and by category, fruits or vegetables, for words) but only in response to items that were presented in the sequence. Results showed that left-handed responses were faster when reacting to items early in the sequence and right-handed responses were faster for items later in the sequence, independent of the type of information that was maintained. They conclude that items in a sequence are placed on a mental spatial template based on their ordinal position in the sequence. More specifically, this implies that items early in the sequence are bound to left space while items later on in the sequence are bound to right space.

Follow up studies have shown that the spatial effect was not limited to a response bias but could also interact with attention. Using a Posner cueing paradigm, van Dijck, and colleagues (2013, 2014) showed that serially presented numbers or letters that were maintained in memory would shift attention from left to right based on the items' ordinal position. Moreover, retrieval of items early and late in a sequence can be facilitated by directing attention to the left or right side of space respectively (de Belder, Abrahamse, Kerckhof, Fias, & van Dijck, 2015). Rinaldi, Brugger, Bockisch, Bertolini, & Girelli (2015) found more evidence that visuospatial attention is used at serial recall. They found that retrieval of items in working memory affected spontaneous eye movements in function of the ordinal position of items in the sequence. Taken together, these studies show a clear relationship between serial order working memory and spatial processing on a horizontal axis in support of the view that position markers are spatial in nature.

It is assumed that the spatial default context of this spatial coordinate system is horizontal, from left to right. However, this spatial system is highly flexible and can seemingly encode items in different spatial configurations. Different spatial biases have been found dependent on the type of items, or the context with which these items had to be memorized; top to bottom (Dutta & Nairne, 1993), right to left (Guida, Abrahamse, & van Dijck, in prep), numeral pad (Darling, Allen, Havelka, Campbell, & Rattray, 2012), or the face of a clock (Bächtold, Baumüller, & Brugger, 1998; Ristic, Weight, & Kingstone, 2006). For example, when instructed to imagine the memorized number(s) on the face of a clock, participants gave faster right-handed responses to numbers on the right side of the clock (number 1 to 5) and faster left-handed responses to numbers on the left side of the clock (number 7 to 11; Bächtold et al., 1998; Ristic et al., 2006). Similarly, in a process called visuospatial bootstrapping, Darling et al. (2012, 2016) found that serial number recall accuracy was improved when the locations of presented numbers matched the spatial location of a typical, numeral pad (as found on a telephone or remote control). These studies show that the spatial configuration with which serial presented items are represented are contextually driven.

The aim of the current study was to examine whether an irrelevant auditory context could influence the spatial context with which serially presented visual items are represented in working memory and whether this would facilitate subsequent item recall. Visual and auditory information can interact in working memory more so than previously assumed (see for a review: Quak, London, & Talsma, 2015). Studies examining multisensory working memory in the audiovisual domain have shown that: a) recall is better for cross-modal objects compared to modality specific objects (Goolkasian and Foos, 2005; Delogu, Raffone, & Belardinelli, 2009; Thompson and Paivio, 1994); b) capacity can be higher for cross-modal objects (Fougnie and Marois, 2011; Saults and Cowan, 2007), and c) that visual and auditory information can interfere with each other (Goolkasian and Foos, 2005; Morey and Cowan, 2004, 2005). More importantly, associations between pitch and vertical locations have been shown to help integrate visual and auditory information for better more effective processing (Cabrera & Morimoto, 2007; Chen & Spence, 2011; Roffler & Buttler, 1968). For example, multiple studies have shown that the pitch of a sound can influence the speed with which locations of visual items are discriminated. Responding to items that were positioned high or low on screen were faster when accompanied by a high or low pitched sound respectively, compared to opposite bindings (e.g., Evans & Treisman, 2010, Patching & Quinlan, 2002). Also, responding to high and low tones was faster when participants had to respond with buttons placed high or low on a response pad (Lidji, Kolinsky, Lochy, & Morais, 2007; Rusconi, Kwan, Giordano, Umilta, & Butterworth, 2006). Similar to the results by van Dijck et al (2013), Chiou and Rich (2012) found that attentional shifts were induced by spatially non-lateralized and non-predictive sounds of different pitches, and that this effect could be flexibly modulated by contextual factors like top-down control and frequency range.

In the experiment presented here we used a 4-item Sternberg task with visually presented Chinese characters in the center of the screen. Participants were instructed to memorize the four Chinese characters in the sequence. After a short retention interval a memory probe was presented and participants indicated with a left or right handed response if the memory probe was part of the initial sequence or not. Left and Right handed responses were used to estimate a participants' spatial bias. Spatial bias is an estimate of how items are represented in space in working memory. It assumes that faster left handed responses are made to items early in the presentation order (ordinal position 1 and 2) compared to later items (ordinal position 3 and 4) and faster right handed responses are made to items later in the presentation order (ordinal position 3 and 4) compared to early items (ordinal position 1 and 2).

To examine whether an auditory context would influence the spatial coding of visual items we created three different auditory contexts: a monotone, an ascending, and a random auditory context. Each Chinese character in the sequence was simultaneously presented with one out of four auditory tones. The tone that was presented at a given point in the sequence was determined by the auditory context. In the monotone context one out of four tones was randomly selected and that same tone was presented with every Chinese character in the sequence. With the ascending condition the four tones were presented in ascending order (from low to high), one with each character presentation. In the random condition each of the four tones was randomly paired with one of the Chinese characters in the sequence. We expected that the monotone context would show a regular left to right spatial bias because the tones were the same on every presentation in a trial giving no extra information. In the ascending context we expected to observe an enhanced left to right spatial bias because the low to high ascending tone sequence elicits a stronger spatial identity in the visual sequence. We expected to observe an inhibited spatial bias in the random context because the random tones give no clear spatial identity to the visual items which could disrupt the spatial processing of the visual items. Lastly, we expected better and faster memory recall in context conditions that show a clear horizontal spatial bias compared to conditions that do not.

METHOD

Participants

In total sixty undergraduate students (mean age 19 years: range 17-23) participated in this study, in exchange for course credit. All participants gave informed consent. In total six participants were excluded from further analyses. Of these six, four were excluded based on below chance level performance on the initial familiarization task and two were excluded based on below chance level performance in the main task.

Materials

Visual and auditory stimuli were presented electronically on a personal computer using the E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA). For the visual stimuli, Chinese characters were selected from a larger stimulus set created by Andrade, Kemps, Werniers, Amy, and Szmalec (2002). In their study Chinese characters were rated on similarity creating sixteen unique character families containing four visually similar characters each. In the current study we used 10 of these characters (Figure 1B), with each character selected from a different character family to keep overlap between different characters to a minimum. Each character was presented in black in the center of the screen against a white background, with a height and width of 3° by 3° in visual angle. On every trial four characters were randomly selected from the pool of ten characters to create a visual stimulus sequence.

Four tones were created using Audacity® version 2.0.5. The pitches of the tones were *A* (440 Hz), *B* (493.88 Hz), *C#* (554.37 Hz), and *D* (587.33 Hz). Duration for each tone was 200 ms, with rise and decay times of 50 ms at the start and end of this interval. These tones were used to create three types of auditory context: (a) a monotone tone sequence, where one of the four tones, randomly selected, was repeated on every visual presentation in a trial, (b) an ascending tone sequence, where the four tones were presented in ascending order, and (c) a random tone sequence, where tones where randomly positioned in the sequence. Tones where presented on a noise-cancelling headphone (Sennheiser HD 215) to the participants at 65 dB.

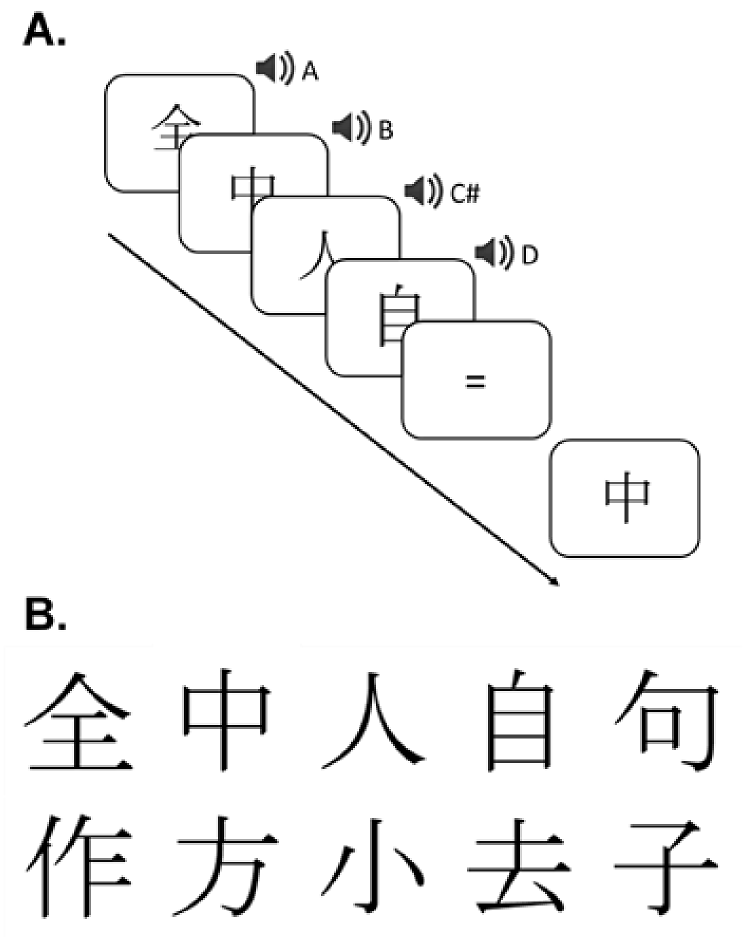

Figure 1. Trial sequence and stimuli. (A) Each trial started with an initial fixation for 1000 ms followed by the presentation of a memory sequence consisting of four randomly selected visual characters presented for 250 ms with an ISI of 750 ms. An auditory tone was presented with each visual character. The memory sequence was followed by a 1000 ms retention interval followed by the memory probe. The memory probe was presented until a response was made. Participants reported whether the memory probe was part of the presented sequence or not. (B) All ten Chinese characters used in the experiment.

Procedure

Participants were seated behind a desktop computer approximately 60 centimeters in front of the monitor. The task started with general instructions explaining the experimental session. The experiment consisted of a familiarization phase, a working memory task, and a concluding questionnaire.

For the familiarization task, participants were presented with 3 blocks of 12 trials. In each block all ten Chinese characters were presented in random order for 1000 ms following a fixation cross in the middle of the screen. Twice during each block a fixation cross would be followed by a red dot in the middle of the screen. Participants were instructed to passively watch the Chinese characters and hit the space bar whenever a red dot appeared. Each familiarization block was followed by a self-paced break.

The memory task started with general instructions explaining the task. Participants were instructed to memorize a sequence of four Chinese characters on each trial. Each sequence was followed by a retention interval after which a memory probe was presented. Participants had to respond to the memory probe by indicating whether the presented item was part of the sequence in memory or not. If the memory probe occurred in the sequence the participant pressed the button corresponding to 'old', otherwise the button corresponding to 'new'.

Each trial started with an initial fixation for 1000 ms followed by the presentation of a memory sequence (see Figure 1A for an overview of the trial sequence). The memory sequence consisted of four randomly selected visual characters presented for 250 ms with an ISI of 750 ms. The onset of each visually presented character in the sequence was synchronized with the simultaneous presentation of an auditory tone. The memory sequence was followed by a 1000 ms retention interval in which an “=” was presented in the center of the screen to distinguish it from the ISI and to alert the participant that the next item presented was the memory probe. The memory probe was presented until a response was made and could either be a ‘new’ item (not presented in the prior sequence) or an ‘old’ item (presented in the prior sequence). Responses were made on a keyboard by pressing either the ‘z’ or ‘m’ key to report a ‘new’ or ‘old’ item, respectively. The stimulus response mapping switched halfway through the experiment and was counterbalanced between participants. After the response a red fixation dot or blank screen was shown for 250 ms to indicate incorrect or correct answers respectively.

The task started with a practice block of 20 trials using each Character twice as a target stimulus (once as an old target and once as a new target). The practice block contained no auditory stimuli. After the first practice block participants were presented with 3 experimental blocks, one for each auditory context (monotone, ascending, and random). After the first three experimental blocks the response mapping switched, participants were instructed on the response change and received a second practice block of 20 trials to get accustomed to the new response mapping. After the second practice block participants received again 3 experimental blocks, one for each auditory context condition. The order of the experimental blocks was counterbalanced between participants. Each block consisted of 40 trials of which half were ‘old’ targets and half were ‘new’ targets for a total of 240 trials.

After the main task participants filled out a concluding questionnaire. The questionnaire contained pictures of all ten Chinese characters used in the main task and participants were asked to indicate whether they used a verbal label to memorize these characters. Participants could write down the label they used for each character.

Analyses

Median reaction times were used to calculate spatial bias because of the wide variation of reaction times between and within subjects. Spatial bias was calculated by subtracting the left handed response to items that were presented early in the sequence (ordinal position 1 and 2) from the right handed response to items presented early in the sequence. This gives a value that represents the difference between left and right-handed responses on items presented early in the sequence. The same difference value was calculated for responses to items late in the sequence (ordinal position 3 and 4) by subtracting right-handed responses from left handed responses. After adding these two difference scores one gets an estimate of spatial bias, where a value of 0 means no spatial bias, or no difference between responses made by left or right hand in light of ordinal position. A positive value would indicate a left to right spatial bias, where participants made faster left handed responses to items early in the sequence and faster right handed responses to items late in the sequence. A negative value of spatial bias would indicate a right to left spatial bias, that participants made faster right handed responses to items early in the sequence and faster left handed responses to items late in the sequence.

In cases where Mauchly's test indicated that the assumption of sphericity had been violated degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity.

RESULTS

Spatial bias

The mean estimates of spatial bias are shown in Figure 2. A one-way repeated-measures ANOVA on Context (monotone, ascending, and random) revealed a significant effect of Context on spatial bias, $F(2, 108) = 4.888$, $p < .009$, $\eta_p^2 = .083$. Pairwise comparisons revealed a significant difference between the monotone and ascending context ($p < .024$) and between the ascending and random context ($p < .005$). There was no reliable difference in spatial bias between the monotone and random context (p =.638). Single-sample *t* Tests were conducted to determine if average spatial bias in each of three auditory contexts was significantly different from zero (no spatial bias). The ascending context elicited a clear left-to-right spatial bias (M = 94.58, SD= 251, SEM = 34), $t(54) = 2,800$, $p < .007$. The spatial biases in both the monotone (M = -17, SD = 285, SEM = 38) and random (M = -38, SD = 260, SEM = 35) context were not significantly different from zero (p's > .4).

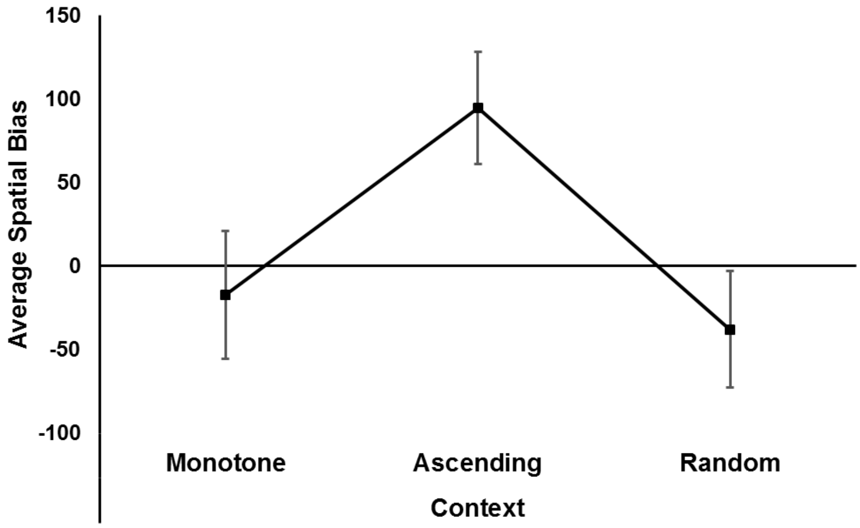

Figure 2. The mean estimates of spatial bias per auditory context. Error bars represent standard error of the mean.

Median reaction times

Average reaction times for Context and Position are shown in Figure 3A. Differences in average median reaction times were analyzed in a 3 (Context: monotone, ascending, and random) x 4 (Position: 1, 2, 3, or 4) repeated measures ANOVA. We observed a significant main effect for Position, $F(3, 159) = 18.315$, $p < .001$, $\eta_p^2 = .257$. Median reaction times were significantly faster when the item at test was presented in the last sequence position compared to third position ($p < .001$), second position ($p < .001$), and first position ($p < .001$). There were no significant differences between test items presented on the first, second, or third position (p's $> .592$). The main effect of Context showed a trend towards significance, F(2,

106) =3.025, $p < .061$, $\eta_p^2 = .054$. Visual inspection of the medians seem to indicate that reaction times tended to be faster in the random auditory context. There was no significant interaction between Context and Position, $F(6, 318) = 1.468$, $p < .189$, $\eta_p^2 = .027$.

Accuracy

Differences in accuracy were analyzed in a 3 (Context: monotone, ascending, and random) x 4 (Position: 1, 2, 3, or 4) repeated measures ANOVA. Average accuracy for Context and Position are shown in Figure 3B. A significant main effect of Position was observed, $F(3, 162) = 54.701$, $p < .001$, $\eta_p^2 = .503$. Accuracy increased when the test item was presented later in the sequence. Pairwise comparisons revealed that accuracy increased significantly when the item at test was presented later in the sequence from position 1 to 2 ($p < .316$), from position 2 to 3 ($p < .001$), and from position 3 to 4 ($p = .001$). The main effect of Context and the interaction between Context and Position were not significant (F's < 1), meaning that auditory context had no effect on average recall accuracy.

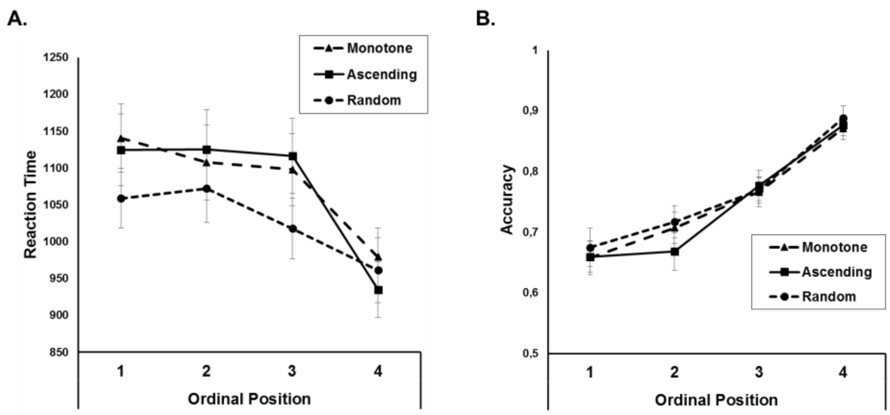

Figure 3. Behavioral results. (A) The effect of ordinal position on reaction time per auditory context. (B) The effect of ordinal position on accuracy per auditory condition. Error bars represent standard error of the mean.

DISCUSSION

In the current experiment we wished to examine whether an irrelevant auditory context could affect spatial processing in serial order working memory and whether this facilitated Sternberg performance. We used median response times on a 4-item Sternberg task with visually presented Chinese characters to estimate spatial bias. There were three types of auditory context that could coincide with visual stimulus presentation: a monotone, ascending, or random context. We expected that the ascending auditory context would cause a more defined or enhanced left to right spatial bias compared to the monotone auditory context which served as a baseline. The random auditory context was expected to disrupt spatial coding of the serially presented items. We expected that a more defined left to right spatial bias would enhance memory performance on the Sternberg task.

Complementary to previous findings of van Dijck and colleagues (2011, 2013, 2014, 2015) the current study shows a relation between serial order working memory and spatial processes. More specifically, we found a clear left to right spatial bias when items in the sequence were simultaneously presented with an ascending auditory context. When items were presented with a monotone or random tone sequence no spatial bias was observed. These findings suggest that the ascending tone sequence was unique in its ability to facilitate the spatial processing of items in working memory. As far as we are aware this is the first study that shows that nonverbal items can be spatially processed, based on the items' ordinal position in a sequence (cf. van Dijck & Fias, 2011). Studies that found spatial processing of serial order items in memory thus far only used verbal items: numbers, letters, and words (van Dijck et al., 2011, 2013, 2014, 2015).

While the ascending tone sequence elicited a spatial bias this did not give a performance benefit over the conditions that did not elicit a spatial bias. Both accuracy and reaction times were not affected any differently between the three conditions. We initially assumed that the spatial processing of items in a sequence would help create a stronger working memory representation but at the moment our results do not support this idea. A possible explanation for these findings is that spatial encoding is simply redundant and that retrieval of these specific items does not rely on spatial scanning in working memory but on other retrieval mechanisms. While we did not find a performance benefit of spatial encoding on item memory it could be that other aspects of working memory that were not specifically tested in the current task did benefit from spatial encoding. It is possible that serial order recall (Darling et al., 2012; Delogu, et al., 2009), free recall (Goolkasian and Foos, 2005; Thompson and Paivio, 1994), or the capacity (cf. Fougnie and Marois, 2011; Saults and Cowan, 2007) of these items improved. It would be worthwhile to examine these effects in the future. Knowing under what circumstances spatial encoding improves or disrupts working memory and examining what aspects of working memory are actually affected could bring new insights on the underlying structure.

It is interesting that we only found evidence of spatial encoding in one of three conditions in the current experiment. In fact, the condition that served as our baseline for performance, the monotone auditory context, did not show any spatial bias. Since there was no condition without an auditory context in the current study we cannot make any claims on whether visual items are automatically processed spatially the same way that verbal items are. We can think of two possible explanations for why only the ascending auditory condition showed evidence for spatial encoding. First, it is possible that the visual items used in the current study are not automatically encoded in space based on their ordinal position. In this case, the ascending auditory context gave a unique context that induced spatial processing in that condition. Second, it is also possible that the visual items used here are in fact automatically spatially processed but that both the monotone and random auditory context interfered with this form of processing. While we are unable to distinguish between these explanations based on the current experiment, we can speculate on why the ascending tone context induced spatial processing or did not interfere with it.

The ascending auditory context was the only context in which the tone sequence was both predictable (the same tone sequence on every trial) and informative (each visual character in a sequence was presented with its own unique tone). The predictable and informative characteristics of the tone sequence might have facilitated the integration of visual, auditory, and spatial order information. Indeed, it has been shown that multisensory integration is affected by top-down processes such as learned associations (Fiebelkorn, Foxe, & Molholm, 2010), attention, and predictability (see Talsma, 2015; Talsma et al., 2010 for reviews). For example, Fiebelkorn et al. (2011) have shown that facilitation of an auditory stimulus in a visual-target detection task only occurred when participants could accurately predict the co-occurrence of the auditory and visual stimulus. Likewise, in the current study spatial encoding might have been elicited only when participants could predict the tones that would occur on each ordinal position, which was impossible in the random auditory context. Therefore, in the random sequence, the variability among the tones may be too unpredictable for them to be bound together into an audiovisual object, which may, in turn, diminish the effectiveness of the auditory stimuli for facilitating spatial coding in working memory. But predictability alone cannot fully account for the effects we found. The monotone condition was also predictable but did not elicit spatial coding. Although both predictable, the ascending and monotone context differed on how informative each tone was in the sequence. In the ascending tone sequence each tone was unique which made each event (the simultaneous presentation of tone and visual item) in the sequence distinctive. It is known that an items' bottom-up distinctiveness plays an important part in visual attentional selection and subsequent processing (see for a review: Fecteau & Munoz, 2006). Similarly, it has been shown that item distinctiveness is a key factor in multisensory integration (see for a review: Spence & Driver, 2004). For example, research has shown that salient auditory stimuli automatically integrate with concurrently presented visual stimuli and orient attention to its physical location (Van der Burg, Olivers, Bronkhorst, & Theeuwes, 2008). This shows that audiovisual integration processes can facilitate spatial processing. Both item predictability and item distinctiveness have been shown to facilitate spatial orienting and multisensory integration, and can help explain why evidence for spatial encoding was only found in the ascending context condition.

It should be mentioned that we cannot rule out that spatial processing took place on the basis of an absence of a left-to-right spatial bias. Although we did not observe the assumed default left-to-right spatial processing, it is possible that the random and monotone context facilitated other spatial configurations, for example top to bottom ones. Most studies that showed a relation between auditory pitch and spatial processing found effects on a vertical axis (e.g., Evans & Treisman, 2010, Patching & Quinlan, 2002; Lidji, et al., 2007; Rusconi, et al., 2006; Chiou and Rich, 2012). Indeed, the fact that behavioral performance as measured with reaction times and accuracy did not differ between conditions seems to imply that the characters were represented as equally strong across conditions. Follow-up research could test the presence of other spatial configurations based on different auditory contexts.

We would like to acknowledge that in the ascending condition, the pitch of the auditory stimulus was confounded with ordinal position. Each ordinal position was always presented with the same unique pitch in ascending order, low pitches early and high pitches late. Lidji, et al. (2007) have shown that pitch can interact with spatial locations in a horizontal space under certain circumstances. It is therefore possible that the response bias found in the ascending context was elicited because the auditory tone was automatically retrieved when an item on test matched an item in the sequence, evoking faster left or right-handed responses based on the pitch. In this case that would create the exact same effect, faster left handed responses on low pitch items (early in the position) and faster right handed responses on high pitch items (late in the position). To partially rule out the possibility that pitch influenced performance by itself in the ascending condition we did an additional analyses on the random condition. The random condition allowed us to look at the effects of pitch separate from ordinal position. We calculated spatial bias in the random condition by using pitch instead of ordinal position. This analysis showed that pitch in itself did not elicit a left-to-right spatial bias (M = -20.85, SD= 375.09, SEM = 50.58), $t(54) = -0.412$, $p = .682$, further supporting our conclusion that the found spatial bias was based on the ordinal position in combination with the ascending auditory context.

In conclusion, the current data shows that processes responsible for the spatial recoding of nonverbal items in serial order working memory can be influenced by an irrelevant auditory context. We found a spatial bias based on the ordinal position of an item presented in a sequence but only when items co-occurred with an ascending auditory tone sequence. This seems to indicate that the auditory context needed to facilitate this repositioning has to consist of informative and predictable auditory stimuli. Although spatial encoding took place when presented with an informative and predictable context this did not improve item memory performance. Under which circumstances spatial encoding does improve memory retrieval is an interesting question for future research. The current study adds to the growing literature that shows that information from different modalities as well as long-term representations can interact in working memory beyond what was previously assumed and underscores the importance of examining multisensory interactions in working memory.

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CHAPTER 5
A MULTISENSORY PERSPECTIVE OF WORKING MEMORY [1]

Although our sensory experience is mostly multisensory in nature, research on working memory representations has focused mainly on examining the senses in isolation. Results from the multisensory processing literature make it clear that the senses interact on a more intimate manner than previously assumed. These interactions raise questions regarding the manner in which multisensory information is maintained in working memory. We discuss the current status of research on multisensory processing and the implications of these findings on our theoretical understanding of working memory. To do so, we focus on reviewing working memory research conducted from a multisensory perspective, and discuss the relation between working memory, attention, and multisensory processing in the context of the predictive coding framework. We argue that a multisensory approach to the study of working memory is indispensable to achieve a realistic understanding of how working memory processes maintain and manipulate information.

[1] Quak, M., London, R. E., & Talsma, D. (2015). A multisensory perspective of working memory. *Frontiers in human neuroscience*, 9, 197.

INTRODUCTION

In everyday life we experience a continuous stream of information that we perceive through sight, sound, smell, taste, and touch. Even though this experience is mostly multisensory, that is, we receive information from multiple senses simultaneously, psychological research has primarily focused on studying our senses in isolation. While we are beginning to understand how our senses interact at various stages of processing (for an overview see, e.g., Beauchamp, 2005; Ghazanfar & Schroeder, 2006; Klemen & Chambers, 2011; Wallace, Meredith, & Stein, 1993; Stein & Stanford, 2008) it is still heavily debated whether the higher-order mental representations that are derived from these sensory inputs still contain modality- specific information or not. For instance, in working memory, research has focused on resolving whether information is memorized in the form of separate, modality or domain specific representations (Baddeley & Hitch, 1974; Schneider & Detweiler, 1987), or as integrated representations (Atkinson & Shiffrin, 1968; Cowan, 2001).

Multisensory processing refers to the interaction of signals arriving nearly simultaneously from different sensory modalities. This implies that information from one modality can influence information processing in another modality. Information from different sensory modalities can also be combined into a single multisensory event, a process that is referred to as multisensory integration (Stein et al., 2010). In accordance with the suggestions of Stein et al. (2010) we will use the terms “modality-specific” or “cross-modal” when describing the properties of objects and “unisensory” or “multisensory” when referring to neural or behavioral processes associated with a single or multiple sensory modalities.

The aim of this paper is to discuss the current status of research on multisensory processing and the implications of these findings for our theoretical understanding of working memory. To do so, we will focus on reviewing working memory research conducted from a multisensory perspective. We will argue that a multisensory approach to the study of working memory is indispensable to achieve a realistic understanding of how working memory processes maintain and manipulate information.

WORKING MEMORY AND THE MULTISENSORY BRAIN

In their seminal work, Atkinson and Shiffrin (1968) devised a model for the flow of information in human memory, which subsequently became known as the modal model. They suggested that environmental information is processed by various modality-specific sensory registers before it is combined into a single, modality-independent, or more formally *amodal*, percept and transferred into a short-term store. According to this view, the short-term store is an amodal, general-purpose mechanism. Atkinson and Shiffrin referred to this mechanism as “working memory”, as it was considered to be responsible for a variety of operations, such as the selection, manipulation, and rehearsal of the memorized items.

A few years later, Baddeley and Hitch (1974) proposed a multiple-component model of working memory where information is assumed to be stored in two domain-specific subsystems (the phonological loop and the visuo-spatial sketchpad) that are directed by a general control mechanism (the central executive). The phonological loop is responsible for short-term maintenance of speech-based and acoustic items. The visuo-spatial sketchpad maintains visually and/or spatially encoded items. In contrast to Atkinson and Shiffrin's (1968) idea of a domain-independent (i.e. amodal) store , Baddeley and Hitch (1974) assume that information (e.g., verbal or spatial) is maintained in its corresponding domain-specific store.

Over the years it has become clear that information from different domains showed more interaction in working memory than one would expect from a strongly domain-specific perspective (e.g., Jiang, Olson, & Chung, 2000; Logie et al., 2000; Prabhakaran, Narayanan, Zhao, & Gabrieli, 2000). An episodic buffer was added to Baddeley and Hitch's (1974) original working memory model to account for, amongst other things, the apparent interaction between phonological and visual processes (Baddeley, 2000). The episodic buffer can be conceived as an amodal storage component, which was estimated to hold up to four chunks of information. Additionally, it was proposed to act as a link between all the other working memory components described above. For this revised model, Baddeley (2000) suggested that the episodic buffer integrates memory traces that may originate from different senses into a coherent perceptual scene.

On the basis of several studies, Postle (2006) has proposed that the brain areas involved in sensory perception are also responsible for the short-term storage of sensory information. For instance, functional magnetic resonance imaging (fMRI) studies showed object-specific memorization effects for faces in the posterior fusiform gyrus (e.g., Druzgal & D'Esposito, 2003; Ranganath, DeGutis, D'Esposito, 2004), an area considered to be vital for face recognition. Postle and D'Esposito (1999) found activity related to memorization of visual object location and depiction in ventral temporal and occipital visual brain areas. Similarly, event-related potential (ERP) modulations can be seen in posterior and occipital recording sites during short-term memorization of visual objects contralateral to the to-be-remembered objects (e.g., Klaver et al., 1999; Vogel & Machizawa, 2004). Such findings (for an overview see, D'Esposito & Postle, 2014; Postle, 2006) indicate that memorizing modality-specific sensory information involves the same brain areas as those involved in the initial sensory processing of that information. This idea is compatible with the classical view that integration of the senses would take place at a later stage of processing, after initial unisensory processing has taken place (see Talsma, in revision, for a discussion). Indeed, using neurophysiological methods with animals (e.g., Fuster, Bodner, & Kroger, 2000; Wallace, Meredith, & Stein, 1993) and fMRI with humans (e.g., Beauchamp, Lee, Argall, & Martin, 2004; Calvert, Campbell, & Brammer, 2000; Wright, Pelphrey, Allison, Mckeown, & McCarthy, 2003) several higher-order brain areas have been identified that seem to be dedicated to integrating information from multiple unisensory sources. Brain areas typically regarded as multisensory in the human brain can for example be found in the lateral occipital-temporal cortex, such as the superior temporal sulcus (STS; Beauchamp, 2005).

An increasing number of studies now suggest, however, that multisensory processing can already take place in brain areas that were considered to be strictly unisensory (see for a review, Foxe & Schroeder, 2005; Macaluso & Driver, 2005). For example, Giard and Peronnet (1999) found multisensory ERP effects as early as 40 ms post-stimulus over occipital scalp areas, suggesting that multisensory interactions take place much earlier than previously assumed. Using fMRI, Foxe et al. (2002) showed integration related effects of auditory and somatosensory stimuli within a region of the auditory cortex previously thought to be unisensory. This brain area was more strongly activated by multisensory stimuli than what might be expected on the basis of a mere summation of either auditory or tactile stimulation alone. Likewise, Dione et al. (2010) found increased BOLD signal in the right primary somatosensory cortex during a delayed sensory-to-motor task for cross-modal visual-somatosensory stimuli compared to modality-specific stimuli.

These findings also have implications for the memorization of multisensory information. If indeed, as Postle (2006) proposes, the brain areas responsible for perceptual processing are the same as those involved in memorization, and if multisensory effects can already be observed in the primary sensory cortices, then we would expect that cross-modal information is stored as a unified representation in working memory. We specifically aim to focus on the questions regarding how multisensory information is encoded in working memory and whether we memorize the individual unisensory representations separately and integrate them at a later stage, or whether they are memorized as part of an integrated, multimodal representation instead.

FEATURE BINDING IN WORKING MEMORY

To fully understand the importance of considering working memory from a multisensory perspective, it is necessary to discuss how information is organized within working memory. An important question here is whether each feature of an object is remembered separately or not (e.g., Diamantopoulou et al., 2011; Klaver et al., 1999; Luck & Vogel, 1997;

Wheeler & Treisman, 2002; Luria & Vogel, 2011; Luria, et al., 2010; Olsson & Poom, 2005; Vogel, McCollough, & Machizawa, 2005; Vogel, Woodman, & Luck, 2001). For example, Luck and Vogel (1997) used a change detection task to examine the capacity of working memory for visual objects. Participants were presented with an array of stimuli, which they had to remember during an interval without the stimuli being present. After this retention interval a second array was presented and participants responded by indicating whether any visual changes had occurred between the second and the first array. Varying the number of visual objects that need to be memorized allows estimating the capacity of visual working memory. Luck and Vogel (1997) found that capacity was limited to approximately four objects, regardless of the number of feature dimensions, or individual features that needed to be remembered per object. This led them to conclude that visual working memory has an object-based and not a feature-based organization. It is important to note that these findings have not been replicated (Hardman & Cowan, 2014; Oberauer & Eichenberger, 2013). At the very least this suggests that feature binding can, but does not always, occur automatically.

Interestingly, research has shown that an asymmetry exists in binding the visual and spatial features of an object. Multiple studies have shown that processing the visual features of an object automatically bind this object to its spatial location (e.g., Jiang, Olson, & Chung, 2000; Olson & Marshuetz, 2005). However, processing an object's spatial location does not result in the automatic binding of that object's visual features (Jiang, Olson, & Chung, 2000). While these findings show that binding of multiple features can occur within the visuo-spatial domain, other studies have shown that binding of features can even occur across domains.

Prabhakaran, Narayanan, Zhao, and Gabrieli (2000) showed that participants memorized verbal and spatial information in an integrated fashion. Participants in this study performed faster and more accurate on a verbal-spatial delayed-match-to-sample task when the probe was a letter-location combination that was presented together in the sample array compared to a letter-location combination that was presented separately. The findings on binding of verbal and spatial information have been replicated and extended in multiple studies (Bao, Li, & Zhang, 2007; Campo et al., 2008, 2010; Elsley & Parmentier, 2009; Guérard, Morey, Lagacé, & Tremblay, 2012; Meier, Nair, Meyerand, Birn, & Prabhakaran, 2014). For example, Bao, Li, and Zhang (2007) found that switching attention between verbal and spatial features was faster when they were features from one object than when they were features from separate objects. Additionally, Guérard et al. (2012) showed that phonological similarity of verbal material can carry over to the recall of spatial locations in a combined verbal-spatial serial recall task. Participants were sequentially presented with letters in specific locations and were asked to either recall the order of spatial locations shown or the order of letters shown. They found that the harmful effect of phonological similarity on verbal recall carried over to spatial recall, but that the harmful effect of spatial complexity on spatial recall did not carry over to verbal recall. While the question remains under which exact circumstances automatic binding or integration of cross-domain information occurs, the asymmetry found in visual feature and location binding as well as verbal and spatial binding, suggest that the automatic integration of information across domains can occur.

MULTISENSORY WORKING MEMORY REPRESENTATIONS

Despite the evidence for integration of information from different domains, surprisingly little research has examined how multisensory information is represented in working memory. One of the first studies to use cross-modal stimuli was done by Thompson and Paivio (1994). Participants memorized three different types of items: visual, auditory, or audiovisual for a later free-recall test. Thompson and Paivio found an improvement of free recall of cross-modal audiovisual stimuli compared to modality-specific, audio or visual stimuli. This superior audiovisual performance was not simply due to the double presentation of information in audiovisual conditions (audio and visual dual presentation), because picture-picture and sound-sound dual presentation conditions did not yield a similar improvement. When pictures in the picture-picture dual presentation condition were two different exemplars of the same item a slight improvement in free recall was found but audiovisual performance still resulted in higher recall rates. Goolkasian and Foos (2005) also found that recall rates were higher for picture/spoken word and written/spoken word dual presentation conditions compared to the double visual presentation of pictures and written words. These findings suggest that the improved memory performance is due to the combination of information from different modalities and not because of the redundancy of the information itself.

In the multisensory literature, additive effects, such as for example linear increases of brain activity for multisensory stimuli (For an overview see; Calvert, 2001), are considered to be exemplary of multisensory processing. By contrast, in working memory research, similar additive effects, such as an increase in capacity for audiovisual material compared to modality-specific material, are considered evidence for the independence of the two modalities. For example, the advantage of cross-modal object recall, in the study of Thompson and Paivio (1994) was explained by Paivio's "dual coding" theory (1971, 1986). This theory states that a memory trace for a cross-modal stimulus is a combination of the independent sensory traces that were encoded, which in turn can be recalled separately when the task so requires. While information from different modalities can interact to provide certain behavioral benefits, this information is in fact independent.

Originally, the dual coding theory was developed to explain the independent, simultaneous processing of verbal and non-verbal information, but has later also been used to explain the independent, simultaneous processing of auditory and visual information. It is important to note that these forms of information can interact. Verbal information can be both visual (e.g., written words) and/or auditory (e.g., spoken words), and nonverbal information can also be visual (e.g., complex visual scenes) and/or auditory (e.g., white noise). We can make a distinction between the format of a working memory representation, i.e. the sensory modality in which the information is perceived and/or processed (e.g., auditory – visual), and the content of the representation, i.e. the actual information that is transferred (verbal - nonverbal). For example, when memorizing an array of blue squares or a picture of a cat, it might be more efficient to memorize this verbally as the verbal code “blue squares” or “red cat”. However, when the task requires one to describe the exact spatial location of each square, or point out a specific cat in an array of red cat pictures, it would be more efficient to use a visual code. We assume that information is processed in the format code that is most optimal for the current task. This implies that multiple format codes might be used for one and the same object, if that is more effective for memorizing that object.

Delogu, Raffone, and Belardinelli (2009) investigated how verbal and non-verbal auditory, visual, and audiovisual material is encoded in working memory. Participants were tested on immediate serial recall for sequentially presented visual, auditory, or audiovisual stimuli in either a non-verbal or verbal condition. In the non-verbal condition, stimuli were either pictures, environmental sounds, or a combination of both, and in the verbal condition, stimuli were either written words, spoken words, or a combination of both. Results showed that in the non-verbal condition serial recall for audiovisual stimuli was higher than recall for auditory or visual stimuli. In the verbal condition, recall for audiovisual material was still higher than recall for visual material, but auditory and audiovisual recall did not differ. The authors also found that preventing participants from articulating reduced memory performance in both the verbal and non-verbal conditions. This suggests that both in the verbal and in the non-verbal presentation conditions, the actual content of the representation was encoded in a verbal code. Furthermore, the verbal content seemed to play a key part in memorizing the stimuli in all conditions. This shows that the format in which information is presented is not necessarily the format in which the information is encoded. For example, when a participant is presented with an auditory stimulus of a meowing cat, it is possible that this sound calls forth a picture of a cat, or the word ‘cat’, which is then kept in working memory instead of the auditory features of the original meowing sound that was presented. It is a requirement that the participant recognizes the presented sound as the meowing produced by a cat in order to ‘recode’ the sound into a visual or verbal representation. This requires semantic information from long term memory to be integrated with the working memory representation. Delogu et al. (2009) concluded that their findings are compatible with Baddeley’s working memory model (2000) where the existence of an episodic buffer integrates information from different modalities and combines this with semantic information from long term memory. Other studies have also shown the influence of semantic information from long term memory on visual working memory object representations (e.g., Diamantopoulou, et al., 2011; Olsson & Poom, 2005) suggesting that information outside the pure visual domain can affect early visual object working memory. Similarly, Darling, Allen, Havelka, Campbell, and Rattray (2012) found that accuracy on a digit serial recall task improved when the locations of presented digits matched the spatial configuration of a typical, numeral keypad (as found on a telephone or television remote) in a process they call visuospatial bootstrapping. They confirmed that this effect was due to the integration of the typical keypad representation from long-term memory with the working memory representation and not only to the binding between verbal and spatial information.

Thus far, the main goal of the studies discussed above was to provide insights into the dual code theory (Paivio, 1971, 1986) and/or the multiple component theory (Baddeley, 2000; Baddeley & Hitch, 1974) mainly by looking at recall performance for a wide variety of stimuli. To better understand how multisensory information interacts in working memory we can look at working memory capacity for cross-modal objects. As mentioned before, estimates of working memory capacity for features and objects have been used to infer that visual working memory representations are object based (Luck & Vogel, 1997). Likewise, by assuming that not only features within a modality but also across modalities are integrated into object representations, examining the number of cross-modal objects one can hold in memory compared to modality-specific objects could give insight into the organization of multisensory working memory. For instance, Saults and Cowan (2007) found that working-memory capacity for audiovisual material can exceed working-memory capacity for modality-specific material under certain conditions. In a series of five experiments, participants were presented with visual arrays of four to eight colored squares and auditory arrays of four spoken digits. They were instructed to memorize the visual array, the auditory array, or both. Interestingly, the performance advantage for audiovisual arrays disappeared when masks were used to block access to previously formed sensory memory traces. In this case, capacity for cross-modal stimuli was as high as the capacity of the highest modality-specific object, indicating that memory traces from an accessory sensory memory (echoic and/ or iconic memory) contributed to the improvement of task performance. Since auditory and visual information did not additively contribute to memory performance when sensory memory traces were excluded, Saults and Cowan (2007) concluded that auditory and visual information share a common storage. Fougnie and Marois (2011) contested this interpretation by arguing that the formula used by Saults and Cowan (2007) to estimate the maximum number of object representations one can hold in working memory, might not adequately reflect the combined capacity of modality-specific stores. Fougnie and Marois argued that one item of auditory information generally places a larger load on memory than one item of visual information, suggesting that these modality-specific differences should be weighted accordingly in such a capacity estimate. Using an adapted formula in a series of three experiments, they found that even when using masks to exclude contributions of sensory memory traces, capacity for cross-modal items was superior to the capacity for modality-specific items. Contrary to Saults and Cowan (2007), they concluded that auditory and visual objects were stored in their own respective stores and contributed to performance without interfering.

Overall, there seems to be a performance benefit for the memorization of audiovisual stimuli compared to the memorization of modality-specific stimuli. It remains under debate, however, whether this benefit exists because these stimuli are integrated into a new amodal representation or because the independent storage of auditory and visual information contributes to performance in an additive fashion because they do not interfere. At this time the same effect is used to argue for both sides of the debate. Where some see the additive performance of audiovisual objects as proof for an interaction or even integration of information in working memory (e.g., Delogu, et al., 2009), others see it as proof that sensory information is memorized in its own separate store (e.g., Fougnie & Marois, 2011).

In addition to examining performance benefits for the combination of auditory and visual processing, we can also study the disruption of processing for the combination of auditory and visual information. In traditional working memory research, interference paradigms have been used to show a double dissociation between two separate processing mechanisms. Meaning that when two processes use the same underlying system, interference will occur which impairs performance on both processes. The disruption of performance between modalities is referred to as cross-modal interference and would suggest that information from the different modalities interact at a certain level. For multisensory working memory this could mean that information from different modalities is maintained in a single, multisensory store. Evidence for cross-modal interference is still somewhat ambiguous, however. For instance, using a visual-pattern-recall and auditory-digit-recall dual task, Cocchini et al. (2002) did not find evidence for cross-modal interference on performance accuracy in working memory. The absence of such interference suggests that working memory operates in a domain-specific manner and is in accordance with the notion of parallel processing without interaction of information from different modalities. In contrast, Goolkasian and Foos (2005) showed that spoken words could interfere with the recall of pictures and written words when using long sequences of incongruent dually presented items. Likewise, Morey and Cowan (2004, 2005), did find cross-modal interference on performance accuracy when memory load was sufficiently high. They examined digit span using a verbal-visual dual task and found that participants showed interference for visual memory recall but only when the verbal load was sufficiently high (a load of 7 digits instead of 2). The interference patterns observed in audio-visual dual tasks are as of yet inconclusive on whether visual and auditory information share a limited capacity storage. Although interference paradigms could give us an answer on the question of whether information from different modalities share a limited capacity storage or not, they cannot answer whether the information from different modalities is integrated in this single storage, or maintained as independent modality-specific traces.

Thus far, research on multisensory working memory has shown that recall is better for cross-modal objects compared to modality-specific objects (Delogu et al., 2009; Goolkasian & Foos, 2005; Thompson & Paivio, 1994), working memory capacity is higher for cross-modal objects under certain circumstances (Fougnie & Marois, 2011; Saults & Cowan, 2007), and visual and auditory information can interfere with each other (Goolkasian & Foos , 2005; Morey & Cowan, 2004, 2005) but not always (Cocchini et al., 2002). Although a performance benefit for cross-modal objects is seen as evidence for integration in multisensory research, in working memory research it has traditionally been seen as evidence that modality-specific information from cross-modal objects is stored in separate stores. While we cannot definitively conclude that cross-modal objects are stored as fully integrated objects in working memory, it is apparent that cross-modal information interacts in working memory beyond what would be expected from modality-specific stores. The question is: at what stage or stages in the processing stream do these interactions occur?

MULTISENSORY PROCESSING, SELECTIVE ATTENTION, AND WORKING MEMORY

To answer this question we turn to research on multisensory processing and selective attention. The insights gained from this research could also inform questions about working memory for multisensory stimuli.

In fact, more and more researchers have challenged the idea that working memory and attention are two separate systems (Awh, Vogel, & Oh, 2006; Cowan, 2001; Oberauer & Hein, 2012; Olivers, 2008; Kiyonaga & Egner, 2013, Klaver & Talsma, 2013). For example, Olivers (2008) reviews evidence for the notion that working memory and attention share the same capacity, content and control processes, suggesting they might be two aspects of the same process. Likewise, Kiyonaga & Egner (2013) discuss the literature that examined the effects of external attention on working memory representations, as well as, the effects of working memory representations on directing selective attention. These studies indicate that a competitive interaction between working memory and selective attention exists, implying that they share a limited resource. Kiyonaga and Egner (2013) state that attention and working memory should no longer be regarded as two separate concepts, but instead as one concept, where attention can be directed externally (selective attention) and/ or internally (working memory). The idea of working memory as internal attention is in line with Cowan’s (2001) original idea of working memory where a capacity limited focus of attention can shift between different levels of processing.

Given the above mentioned observations that working memory and attention are presumably two different aspects of the same underlying process, and considering that several studies have shown close ties between attention and multisensory processing, it is necessary to understand the implications of these ties for working memory. Instances where multisensory events guide and focus attention (also referred to as bottom-up effects) suggest an early integration of multisensory information, while instances where attention is needed for multisensory integration (also referred to as top-down effects) are indicative of late integration processes. There is evidence for both types of interaction between multisensory integration and attention. Factors that determine the predominance of either early and/or late interactions between information from different modalities are for example, task-relevancy (e.g., Busse, Roberts, Crist, Weissman, & Woldorff, 2005), learned associations (e.g., Molholm, Martinez, Shpaner, & Foxe, 2007), and saliency (e.g., Van der Burg, Olivers, Bronkhorst, & Theeuwes, 2008).

An example of top-down influence of attention on multisensory integration was given by Talsma and colleagues (e.g., Talsma & Woldorff, 2005, Talsma, Doty, & Woldorff, 2007; Senkowski, Talsma, Herrman, Woldorff, 2005). Using a rapid succession of task-relevant and irrelevant stimuli, they found that attention could influence the integration of cross-modal stimuli. Similarly, Alsius and colleagues (Alsius, Navarra, Campbell & Soto-Faraco, 2005; Alsius, Navarra, & Soto-Faraco, 2007) have shown that attending elsewhere diminishes participants susceptibility to the McGurk illusion (McGurk & MacDonald, 1976). Based on these findings it appears that attending to the relevant, to-be-integrated stimuli is necessary to build a robust, integrated representation (Talsma, Senkowski, Soto-Faraco, & Woldorff, 2010).

However, evidence for bottom-up modulation of attention by multisensory integration has made it clear that multisensory processing can already happen in very early stages of perception (Giard & Peronnet, 1999; Molholm et al., 2002; Van der Burg, et al., 2011). For instance, Van der Burg et al. (2011) presented dynamic displays consisting of line elements that randomly changed orientation. When a target orientation change was synchronized with a short, spatially uninformative tone, visual search was strongly facilitated as compared to when the tone was absent. The interpretation given to these results was that the tone and the synchronized orientation change were bound together into one coherent event, thereby forming a cross-modal singleton that “popped out” between the non-synchronized visual distractors. EEG data showed that this multisensory benefit was apparent as early as 50 ms post-stimulus onset and that the strength of this effect predicted the magnitude of the behavioral benefit during visual search, due to the auditory signal.

The findings above imply that both top-down (task-relevance and learned associations) as well as bottom-up (salience) processes are involved in multisensory integration. To resolve this apparent contradiction between a bottom-up view of multisensory processing, where early multisensory effects seem to *drive* attention, and a top-down view of multi-sensory processing, where attention seems to be *required* to integrate cross-modal objects, Talsma et al. (2010) proposed a unified framework of attention and multisensory processing. According to this framework, early pre-attentive processes can bind multisensory inputs together, but only when competition among the individual inputs is low. Thus, the early latency processes serve to cross-feed low-level information between the individual sensory cortices involved in the integration processes. Early interactions might serve to realign auditory and visual input signals. Auditory information might give temporal information to visual cortex whereas visual information might provide spatial information to auditory processing.

This pre-attentive early integration would, according to Talsma et al. (2010), only be possible, however, if the stimuli presented in one modality do not need to compete for processing capacity with other stimuli in that same modality. If there is competition among multiple stimuli in one modality, top-down attentional control may be required to filter out any stimulus that is not task relevant, thereby prioritizing those stimuli that are task relevant. Consistent with this view, Van der Burg, Olivers, and Theeuwes (2012) found that the earlier mentioned automatic capture by a synchronized cross-modal event can be modulated by the size of the attentional window, meaning that when participants were less focused the effect of the cross-modal pop out was stronger than when participants were forced to focus on a small cue before the synchronized cross-modal event. In conclusion, stimulus-driven, bottom-up processes can automatically capture attention towards multisensory events. Top-down attention can in turn facilitate the integration of multisensory information which leads to a spread of attention across sensory modalities.

Based on the previously mentioned idea that external attention and internal attention (working memory) are two aspects of the same process, findings in attentional research could be applied to working memory. It has been shown that spatial attention can actively influence working memory representations by facilitating encoding (Uncapher, Hutchinson, & Wagner, 2011) and improving the recall of memorized representations (Murray, Nobre, Clark, Cravo, & Stokes, 2013). These effects are found not only within a single modality, but also across modalities. For instance, an auditory cue can draw attention to a visual object and vice versa (Spence & Driver, 1997; Koelewijn, Bronkhorst, & Theeuwes, 2009). Similar effects for working memory have been found by Botta et al. (2011). They examined the effect of visual, auditory, and audiovisual cues on working memory for arrays of colored squares in a change detection task. The cross-modal and modality-specific cues could either capture attention towards the hemifield which contained the to-be-remembered objects, or towards the opposite hemifield which contained the to-be-ignored objects. They found that audiovisual cues had a larger influence on performance accuracy than modality-specific visual or auditory cues. Memory accuracy was increased when an audiovisual cue was presented on the same side as the target and it was decreased when the audiovisual cue was presented on the opposite side. Both the facilitation and impairment of memory performance was larger for audiovisual cues compared to visual cues. Although these data do not directly address the question of how a cross-modal object is represented in working memory as such, they do tell us that multisensory information has a bottom-up effect on the subsequent memorization of a unisensory object.

Investigation of top-down effects of working memory on attention has revealed that working memory content can affect the allocation of visual selective attention (Olivers, Meijer, & Theeuwes, 2006). In a multisensory context, Murray et al. (2004) found that discrimination accuracy of visual objects, presented 20 seconds after initial presentation, improved when the initial presentation was a picture-sound combination compared to a unisensory picture. EEG data revealed that the neuronal response to a cross-modal stimulus happened as fast as 60 to 136 ms and predominantly influenced activation in the right lateral occipital complex. Where a semantically congruent picture-sound combination increased discrimination accuracy on a second presentation, a pure tone decreased discrimination accuracy on a second presentation (Lehman & Murray, 2005; Thelen, Cappe, & Murray, 2012). Thelen, Talsma, and Murray (in press) replicate these earlier findings, while also showing the same effects in the auditory modality. Single-trial multisensory memories affect later auditory recognition. If cross-modal objects were congruent (visual and auditory information match semantically) accuracy was higher compared to unisensory stimuli but became worse if objects were incongruent or meaningless. Unisensory percepts seem to trigger the multisensory representations associated with them, suggesting at least a partially integrated storage in memory. Yet, it seems a multisensory representation stored in memory is only beneficial for memory performance when sounds and pictures are semantically congruent. These studies show that an internal representation is formed in which both the visual and auditory information is encoded. Moreover, they also indicate that information presented in a task irrelevant modality interferes with the task relevant representation. But although this still does not address the question of whether unisensory information is still accessible it does show that the original unisensory representations are closely related. Similar to the findings in research on attention and multisensory integration, it seems that top-down and bottom-up processes play an important part in the integration of cross-modal information in working memory representations.

PREDICTIVE CODING AND MULTISENSORY WORKING MEMORY

One influential framework that can explain the intricacies of top-down and bottom-up interactions in multisensory memory is that of predictive coding. The predictive coding framework states that the brain produces a Bayesian estimate of the environment (Friston, 2010). According to this view, stochastic models of the environment exist in the brain, which are continuously updated on the basis of processed sensory information.

Higher-order brain areas thus provide the lower areas with predictions (or in Bayesian terms “priors”) that influence the processing of ongoing sensory input. A strong mismatch between the prediction and the actual sensory input will then result in a major update of the internal model. Thus when we are in a complex environment with many stimuli competing for processing capacity, incongruence between the top-down predictions of the environment and the present incoming environmental information can determine the priority with which incoming stimuli need to be processed and integrated. The processed information changes the predictions and vise versa. Bottom-up sensory processing and top-down predictions mutually define each other continuously. In this way, the predictive coding view can explain how top-down and bottom-up processes interact in multisensory integration.

Talsma (in revision) recently argued that the dynamic model of our environment provided by the aforementioned stochastic representations is essential to understanding the interaction between basic (multi)sensory processing on the one hand, and memory and attention on the other. For instance, Vetter, Smith, and Muckli (2014) showed that actual auditory stimulation as well as imagined sounds could activate the visual cortex. Based on the predictive coding framework, these authors argued that visual cortex activation came about because either direct sensory information or a stored memory representation thereof could update the internal representation of the sound and therefore indirectly influence processing in visual cortex accordingly. This suggests that attention, memory, and multisensory processing are intrinsically intertwined. Similarly, Berger and Ehrsson (2013, 2014) showed that imagined sounds can mimic the effects of actual sounds in a number of well-known multisensory illusions, such as the bounce-pass illusion (Sekuler, Sekuler, & Lau, 1997), the McGurk effect (McGurk and MacDonald, 1976), or the ventriloquist illusion (Howard & Templeton, 1966), and show independent of each other that visual cortex can be activated both by multisensory stimulation and by memory. Based on these findings, Talsma (in revision) argued that despite the fact that several studies showed that auditory and visual inputs can interact at very early processing stages, the actual integration of the sensory inputs into a coherent mental representation occurs at later, higher-order processing stages.

An important consequence of applying the predictive coding framework is that our internal representation is assumed not only to be built on the basis of direct sensory input, but that it is also updated (and made consistent with) information stored in memory. Thus, attention is assumed to play an essential role in regulating how our sensory input is combined with these pre-existing representations stored in long-term memory. This is largely consistent with Cowan's idea of the focus of attention (2001), which is a part of activated long-term memory, as well as with Baddeley's episodic buffer (2000), although, Baddeley recently argued that attention in the form of the central executive was not necessary for the integration of multiple sources of information in the episodic buffer (Baddeley, Allen, & Hitch, 2011).

A further consequence of applying the predictive coding framework is that the internal representation is by definition always multisensory. Moreover, the active representation integrates all possible sources of information, including semantic information from long-term memory. Thus, even when only a unisensory stimulus is presented, associated representations will be activated as well. These can include information from other modalities, prior experience with the stimulus, or learned associations. Because the formation of this internal mental representation is an active process that influences ongoing processes in the sensory cortices, this model can explain why memory traces in one modality can be strengthened or corrupted by traces in another one. Furthermore, because the active representation sends feedback information to the low-level processes in sensory cortices it can be assumed that the original unisensory memory traces are still present albeit in a relatively fragile state.

MULTISENSORY WORKING MEMORY REPRESENTATIONS IN CURRENT MODELS

The active internal environmental model as proposed by the predictive coding framework would be akin to what we would describe as a multisensory working memory representation. This memory representation does not only consist of information coming from different modalities but also includes information from long-term memory such as semantic knowledge or learned associations. Taking the previously mentioned example of memorizing a cat picture the multisensory representation includes not only the visual features of the cat, but also long-term semantic knowledge of cats, autobiographical knowledge (previous personal experience with cats), and information from modalities not presented with the picture (the sound a cat makes or the knowledge that its fur is soft to the touch). We assume that working memory has an amodal central storage component. Whether this is the main component of working memory as suggested by Cowan (2001) or a part of a bigger system like the episodic buffer in Baddeley's model (2000; Baddeley, Allen, & Hitch, 2011) remains a point for further investigation.

The predictive coding framework would suggest that incoming sensory information is constantly used to update the internal environmental model, implying that incoming stimuli tend to integrate into a coherent multisensory representation. This framework can also explain why working memory is amodal in some cases and modality specific in others. For instance, Postle (2006) argued that working memory for modality-specific stimuli occurs in the sensory cortices. Recently, Yonelinas (2013) suggested that high-resolution bindings are stored in the hippocampus that can be used to support perception and working memory, specifically in memorizing (combinations of) complex features. In the latter case it is plausible that the multisensory representation will be activated, whereas in the former case it is not. Based on this, one important implication of the predictive coding approach is that differences in task and stimulus complexity can yield rather drastically different outcomes. With this in mind a recommendation for future research would be to consider effects of task and stimulus complexity on working memory activation.

Based on the above mentioned framework, we assume that sensory cortices can retain small amounts of modality-specific information (as suggested by Postle, 2006) and that this information supports a multisensory memory representation in higher order areas (e.g., the hippocampus; Yonelinas, 2013). Whether working memory for a specific task involves the higher-order areas or the sensory areas to retain information for limited time depends on the task and the information that needs to be memorized. For example, simple flashes and beeps could be retained in the sensory areas, whereas more complex information would also require the higher-order areas. In that sense the sensory cortices would retain information in a manner similar to separate slave systems (Baddeley & Hitch, 1974) or the recently suggested peripheral storage (Cowan, Saults, & Blume, 2014).

SUMMARY AND CONCLUSIONS

In this paper we have reviewed recent developments in multisensory working memory research. Research has shown that cross-modal information interacts in working memory beyond what would be expected from the traditional modality-specific stores. Recall is better for cross-modal objects compared to modality-specific objects (Delogu et al., 2009; Goolkasian & Foos, 2005; Thompson & Paivio, 1994), working memory capacity can be higher for cross-modal objects than for unimodal objects (Fougnie & Marois, 2011; Saults & Cowan, 2007), and visual and auditory memory can interfere with each other (Goolkasian & Foos , 2005; Morey & Cowan, 2004, 2005). Furthermore, multisensory information has an effect on the subsequent memorization of a unisensory object (Botta et al, 2011) and multisensory memory representations can influence subsequent unisensory stimulus discrimination (Lehman & Murray, 2005; Murray et al., 2004; Thelen, Cappe, & Murray, 2012; Thelen, Talsma, & Murray, in press). Taken together, these studies show that sensory representations in multiple modalities interact more with each other than can be explained by classical modal models.

Paivio’s dual coding theory (1971, 1986) states that although cross-modal information can interact it is in fact independent, because modality-specific information can still be retrieved in isolation. However, studies done by Thelen and colleagues (Thelen, Cappe, & Murray, 2012; Thelen, Talsma, & Murray, in press) show that this retrieval of modality-specific information from a cross-modal representation is more difficult than assumed, because a task irrelevant modality interferes with the task relevant representation. Moreover, higher-order representations of the external world built from memorized information have been shown to influence visual processing. Complex representations seem to be formed in working memory, consisting of the integration of several independent representations that can be sensory, and short- or long-term memory activations. Depending on task requirements either just the simple modal representation or the complex high-resolution binding of several features at once will become active. Therefore, we conclude that working memory is in essence multisensory, and that this must be taken into account to achieve a realistic understanding of how working memory processes maintain and manipulate information.

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CHAPTER 6
GENERAL DISCUSSION

The current dissertation set out to investigate how information from different sources is represented in working memory. One of the key functions of working memory -that has previously been ignored to a large extent in the scientific literature- is that it facilitates the integration of multiple features and representations of our surroundings. In our daily life, we experience the world through different senses and integrate the information stemming from these senses into a coherent representation. Despite the importance of these integrative mechanisms, working memory research has mostly focused on examining information from different modalities in isolation, with some suggesting that information from different modalities is represented in separate stores. Here, the integrative aspects of working memory processes were examined in two different ways. The first part of the dissertation focuses on integration of stimulus features within the visual modality, while the second part focuses on integration across modalities. The first major question we addressed is how individual visual features are represented in working memory and whether these features are integrated into a unified object. In the second part, we address the question how feature-binding processes in working memory can extend beyond the visual domain. More specifically, we examine the influence of auditory information on visual memory processing.

VISUAL WORKING MEMORY REPRESENTATIONS

Whether the number of objects or the total amount of information imposes a limit on visual working memory capacity is still an ongoing debate in visual working memory literature. The object-limited view assumes that visual information is bound together in integrated objects and that a fixed number of these objects can be maintained at the same time (see for a review: Luck & Vogel, 2013). According to this view either all information of one object is represented in working memory or nothing. The information-limited view, on the other hand, assumes that a varying number of objects can be maintained dependent on the precision with which these objects are encoded (see for a review: Ma, Husain, & Bays, 2014).

In Chapter 2 we investigated whether visual objects could be stored in working memory at variable levels-of-detail. We did so by employing a change detection task with novel visual objects that could be memorized with differing degrees of precision. This task-feature allowed us to examine whether participants could employ some strategic control over the amount of detail they memorized per object. The main finding of this study was that visual working memory capacity was significantly affected by the amount of detail that had to be memorized per object. Change detection accuracy decreased not only as a function of the number of objects that were required to be memorized, but also as a function of the required level-of-detail. These two factors did not interact, which could suggest that object and detail information affected change detection performance independently. The results from this experiment imply that memorizing more detail of an object came at the cost of being able to memorize fewer objects. Moreover, our results indicate that participants could strategically control the amount of detail they memorized per object dependent on the task instruction. Although we should be careful with the interpretation, for reasons outlined below, these results are compatible with information-limited models of working memory capacity.

One limitation of the study presented in Chapter 2 is that the three levels-of-detail impose different limitations upon the working memory system. Specifically, memorizing the highest level-of-detail, that is, the spatial structure of each stimulus, may be contingent upon the lowest level; the general shape of the stimuli. To circumvent this problem we devised a new experiment that used a set of stimuli, which consisted of features that were all independent of each other. Using this multi-feature approach, we were able to instruct participants to selectively remember one or more of these features from each object. Moreover, this approach allowed us to investigate whether individual features were represented separately in working memory, or whether they are bound together into integrated object representations. Given the dependency of the different levels-of-detail on each other, this is something that we were unable to do in Chapter 2.

In Chapter 3 we thus examined whether multi-feature objects are represented as separate features or as integrated objects in visual working memory. Specifically, we examined the effect of feature load on visual working memory capacity, change detection sensitivity, and posterior slow wave event-related brain potential (ERP) activity during memory retention using a change detection task with multi-feature objects. In the two experiments we conducted, we found that visual working memory capacity was significantly impacted by feature- as well as by object load, but found no interactions between these factors, suggesting that object and feature load modulated working memory capacity independently. Interestingly, we found a possible dissociation between bilateral and lateralized ERP activity during memorization. Bilateral delay activity decreased in amplitude when more features had to be memorized whereas lateralized ERP activity increased in amplitude when more objects had to be memorized, but only on the contralateral side. Together with the behavioral results, these findings suggest that both object information as well as separate feature information is represented in working memory.

For a long time the dominant view has been that working memory capacity is only sensitive to object load and not the feature load of these objects, and, that objects are maintained with a fixed precision (e.g., Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001; Zhang & Luck, 2008). Clearly, our findings do not support this object-based view. We found that both the precision as well as the number of features of an object affected the number of objects that could be maintained in working memory. This finding is congruent with continuous resource models that assume that capacity is limited by the total amount visual information and the precision with which this information is represented (e.g., Alvarez & Cavanagh. 2004; Bays & Husain, 2008; Wilken & Ma, 2004). We should be cautious, however, to advocate against the importance of object-based representations, because in each of our experiments, our results do indicate that there is a fixed upper limit on the number of objects that can be memorized.

Indeed, it appears that object-representations as well as separate feature-representations contribute to limitations in visual working memory performance. This conclusion fits well with recent studies that have suggested that both object and feature representations are maintained in working memory (e.g., Fougnie, Asplund, & Marois, 2010; Fougnie, Cormiea, Kanabar, & Alvarez, 2016; Vergauwe & Cowan, 2015; Xu & Chun, 2006). For example, using functional magnetic resonance imaging (fMRI) Xu and Chun (2006) found that two separate systems were involved in visual working memory. Activity in the inferior intraparietal sulcus was associated with the number of objects that had to be memorized, with each of these objects occupying a unique spatial location. In contrast, activity in the superior intraparietal sulcus and lateral occipital complex was related to stimulus complexity and the overall amount of visual information that was encoded. These findings resemble our ERP data where we found that posterior contralateral activity was modulated by object load and posterior bilateral activity was modulated by feature load. In line with Xu & Chun (2006) and our results, Fougnie et al. (2010) devised a model that can explain how precision, and object and feature information interact to limit working memory capacity. They assume that when object load increases, the probability that an object is stored and the precision with which the object is represented decreases. The number of features will only affect the precision of information in the encoded objects. Thus it seems that capacity is limited by an upper bound in the amount of objects that can be stored but that within that upper bound capacity can be flexibly allocated depending on item complexity (see for a similar conclusion: Alvarez & Cavanagh, 2004).

To conclude, the studies in Chapters 2 and 3 collectively show that both individual features of an object and the total number of objects determine working memory capacity. First, capacity, as measured by Cowan's *K*, for the same objects decreased when the number of features or precision with which objects had to be memorized increased. Second, in both tasks change-detection performance, as measured by average accuracy (Chapter 2) and *d*-prime (Chapter 3), was affected by object load and feature load. Third, our ERP results indicate a dissociation between bilateral posterior activity (which shows an effect of feature load) and lateralized posterior activity (which shows an effect of object load) during memorization of multi-feature objects. Last, performance decreased when participants were instructed to memorize more information (precision and feature) which suggests that people are able to strategically control how visual information is encoded, maintained, and/ or retrieved. Based on our own findings and in agreement with recent studies in visual working memory literature (e.g., Fougnie et al., 2010; Fougnie et al., 2016; Vergauwe & Cowan, 2015; Xu & Chun, 2006), we assume that both object- and feature representations are simultaneously, and separately maintained in working memory (cf. Fougnie et al., 2010; Xu & Chun, 2006). Moreover, we assume that people have some strategic control over how visual information is encoded and maintained (cf. Fougnie et al., 2016), and retrieved (cf. Vergauwe & Cowan, 2015).

CROSS-MODAL WORKING MEMORY

Recent advances in the field of multisensory processing have questioned the classical notion of modality-specific processing (Ghazanfar & Schroeder, 2006), by showing the existence of very rapid interactions between multiple sensory systems (e.g., Giard & Péronnet, 1999; Talsma, Doty, & Woldorff, 2007), direct pathways between the visual and auditory cortices (e.g., Beer, Plank, & Greenlee, 2011; Falchier, Clavagnier, Barone, & Kennedy, 2002), and demonstrating how early multisensory interactions may contribute to attentional orienting and memorization processes (e.g., Van der Burg, Talsma, Olivers, Hickey, & Theeuwes, 2011; Talsma, Senkowski, Soto-Faraco, & Woldorff, 2010). Following this, a limited number of studies have shown that multisensory processing might affect visual working memory performance. For instance, Botta et al. (2011) showed that multisensory cues were more effective in biasing the access of information in visual working memory than pure visual cues were. Likewise, it has been reported that memory capacity for bimodal stimuli was larger than that of visual or auditory stimuli (e.g., Delogu, Raffone, & Belardinelli, 2009). Further evidence suggesting that working memory is not entirely modality specific, was recently provided by Senkowski, Schneider, Tandler, & Engel (2009), who showed that the binding of visual and auditory features of a memorized object are reflected in high frequency (> 40 Hz) oscillations in EEG waveforms. Taken together, we now have considerable evidence that non-visual processes can exert an influence on visual working memory processes. It remains a question, however, how modality specific codes and more abstract, contextual, forms of information interact in working memory.

Chapters 4 and 5 set out to address that question. More specifically, in Chapter 4 we focused on the question whether an irrelevant auditory context could influence the spatial coding with which serially presented visual items are represented in working memory and whether this would facilitate subsequent item recall. Participants were instructed to memorize visually presented Chinese characters in a 4-item Sternberg task. We created three different auditory contexts: a monotone, an ascending, and a random auditory context. Each Chinese character in the sequence was simultaneously presented with one out of four auditory tones. The tone that was presented at a given point in the sequence was determined by the auditory context. We found that processes responsible for the spatial recoding of nonverbal items in serial order working memory can be influenced by an irrelevant auditory context. We found a spatial bias based on the ordinal position of an item presented in a sequence but only when items co-occurred with an ascending auditory tone sequence. This seems to indicate that the auditory context needed to facilitate this repositioning has to consist of informative and predictable auditory stimuli. Although spatial encoding took place when presented with an informative and predictable context this did not improve item memory performance.

Finally, in Chapter 5 we review the literature on audio-visual interactions and integration in working memory and attention. Despite evidence that has historically argued in favor of modality-specific working memory systems (e.g., Baddeley & Hitch, 1974), Chapter 4 discusses an increasing body of literature suggesting that cross-modal interactions do play an important role in working memory. For example, studies examining multisensory working memory in the audiovisual domain have shown that:

a) recall is better for cross-modal objects compared to modality specific objects (Delogu, Raffone, & Belardinelli, 2009; Goolkasian and Foos, 2005; Thompson and Paivio, 1994); b) capacity can be higher for cross-modal objects (Fougnie and Marois, 2011; Saults and Cowan, 2007), and c) that visual and auditory information can interfere with each other (Goolkasian and Foos, 2005; Morey and Cowan, 2004, 2005). Moreover, the memorization of modality-specific objects is affected by cross-modal cues (Botta et al., 2011) and unisensory object discrimination is affected by a multisensory memory representation (e.g., Murray et al., 2004). These studies indicate that representations in memory can be unisensory or multisensory, and that both top-down and bottom-up processes play an important part in the integration of information. Based on the above-mentioned findings, recent developments in neuroscientific models of working memory (D'Esposito & Postle, 2014; Postle, 2006), and the gaining popularity of the predictive coding framework (Friston, 2010), we concluded that a complex multisensory representation seemed to be formed in working memory, which consists of the integration of several independent representations that can be sensory, and short- or long-term activations. Specifically, we assume that sensory cortices maintain small amounts of unisensory information (cf. Postle, 2006) and that this information supports a multisensory representation in higher-order association areas (Postle, 2006; Yonelinas, 2013).

Our conclusion that multiple representations (e.g., simple unisensory and integrated multisensory) can be maintained at the same time is congruent with our conclusion in the visual domain (Chapter 2 and 3) in the sense that both visual features and integrated objects can be represented simultaneously. In his emergent property view, Postle (2006) suggests two main principles that determine active representations in working memory. First, information maintenance is associated with sustained activity in brain regions that are responsible for the processing of information in non-working memory related situations (e.g., perception). Second, any presented stimulus will activate as many representations as can be afforded by the stimulus. For example, a visually presented cat picture will not only activate visual representations but also long-term semantic and autobiographical knowledge of cats (previous experiences with cats), and possibly, information from modalities not presented with the picture (e.g., the sound a cat makes, or the touch of its fur). Whether working memory performance on any specific task is dependent on the complex multisensory representation or simple unisensory representations is an interesting question for future research. One obvious possibility is that it depends on specific task needs. In the visual domain, two recent studies have shown that either the feature or integrated object representation is active based on the task instructions that participants received (Fougnie et al., 2016; Vergauwe & Cowan, 2015). Similarly, in a cross-modal verbal-spatial task, Morey (2009) found that memory for spatial locations was impaired by a concurrent verbal rehearsal task when participants were required to maintain the verbal-spatial binding, but not when the task did not require verbal spatial binding. Our results are congruent with above-mentioned findings in that we found that participants were able to memorize the same objects with more detail if the task demanded it.

Another possible determinant of whether the simple or complex representation is used is the to-be-remembered stimulus properties. For example, simple beeps and flashes will only activate simple representations while pictures of known objects will activate a complex representation. This could help explain the discrepancy in visual working memory literature on whether features or integrated objects are the main determining factor of capacity. As discussed in Chapter 3, the discrepancy in results might be explained by the difference in visual objects used within and across tasks, where some objects might elicit a form of obligatory binding and others do not. Whether a complex representation is formed of two independent simultaneously presented stimuli will also depend on the stimulus properties. For example, in Chapter 4 we found that a complex audio-visual representation was only formed if the auditory stimulus was both informative and predictable. This is consistent with research in the multisensory integration field, which shows that integration of multiple sources of information is dependent on amongst other things; task relevancy (e.g., Busse, Roberts, Crist, Weissman, & Woldorff, 2005), saliency (Van der Burg, Olivers, Bronkhorst, & Theeuwes, 2008), and predictability (Fiebelkorn et al., 2011). Based on the evidence put forward in the current dissertation, we assume that multiple representations exist in working memory and that the activation of specific representations is in large part determined by task instructions and stimulus properties.

THE FUTURE OF WORKING MEMORY RESEARCH

The current dissertation is not without its limits. While we assume that multiple representations exist in working memory, it is important to note that these assumptions are mostly based on our findings in the visual domain (Chapter 2 and 3) and a review of literature in the audio-visual domain

(Chapter 5). More specific hypothesis testing is required to confirm our assumptions and to determine how this extends to findings in other domains.

In Chapters 2 and 3, the main focus was on whether precision and feature load could affect visual working memory capacity. We found that both precision and feature load decreased the number of objects that could be memorized simultaneously. In Chapter 2, however, the effect of level-of-detail was possibly confounded with test uncertainty due to the nature of the multi-feature objects used and the possible changes that could occur on test. Specifically, when participants had to report a change in the color of an object, reporting that no color change had occurred when the spatial locations of colors had changed was significantly more difficult, as suggested by the increase in errors in this condition. How irrelevant features impact encoding, maintenance, and retrieval in a change-detection task has largely been unexplored with earlier studies showing mixed results. For example, Woodman, Vogel, and Luck (2012) found no evidence that change detection performance was affected by irrelevant size or location changes, while others have shown that irrelevant features affected change detection performance when relevant memory load was low (Xu, 2010), or when the retention interval was short (<500 ms, Logie, Brockmole, & Jaswal, 2010). Comparing relevant and irrelevant information and how they affect working memory performance could be a fruitful line of research to examine information binding in visual working memory.

In both Chapters 2 and 3 we found that both the number of objects and the amount detail (or number of features) memorized per object affected change detection performance. Because we found no interaction between object load and information load we concluded that both affected capacity independently. Although we must be careful to make any strong assumptions based on a null result, we did find the same effect in three separate experiments. Moreover, the dissociation between bilateral and lateralized ERP activity seems to indicate that multiple representations coexist. The dissociation between bilateral and lateralized posterior ERP activity raises some interesting questions. First, it needs to be determined whether the bilateral activity is indeed due to processes in memorization or whether it is an artifact of low level and early perceptual processing as suggested by Vogel and Machizawa (2004). Secondly, if we consider CDA activity to represent integrated objects, could it possibly be influenced by other non-visual sources of information? Although earlier work employing the CDA has emphasized the role of visual brain areas in working memory (e.g., Klaver, Talsma, Wijers, Heinze, & Mulder, 1999; Vogel & Machizawa, 2004), subsequent work has provided reasons to question whether working memory operates on pure modality specific (e.g. visual) contents. Firstly, Diamantopoulou et al. (2011) recently showed that the CDA amplitude is more sensitive to memory load manipulations when the material that is to be memorized consists of multiple discrete categories than when it consisted of visually more demanding continuous variations of the same category. This somewhat counterintuitive result is hard to explain in terms of pure visual processes driving these occipital activations. Thus, this finding was interpreted to imply that the occipital CDA component reflects the association between pure visual processes and a more abstract semantic form of categorical coding, presumably representing a process binding the categorical information to a visual code. If this is the case, then memory involves binding together multiple features and objects. Our results are compatible with these findings in the sense that they also underscore the finding that the CDA is sensitive to other factors than just the storage of individual stimulus features. A potential interesting line of research could examine whether CDA activity represents purely visual integrated objects or whether it is a more general representation of integrated objects that could also contain information from long-term memory and/ or other modalities.

Multisensory Working Memory

Overall, we believe that the study of multisensory working memory could bring important new insights on how working memory processes help integrate information from multiple sources at once to assist in daily functioning. It can help answer the question how and where information in working memory is represented and maintained. One important aspect that has been overlooked in working memory research is the difference between what we earlier described as the format, i.e., the sensory modality in which the information is perceived and/ or processed (e.g., auditory or visual), and the content, i.e., the actual information that is transferred (e.g., verbal or non-verbal), of working memory representations (Chapter 5). For example, a specific cat picture (visual format) can be memorized in multiple ways: a visual representation of the cat picture (visual content), a verbal description of the cat picture (verbal content), or the simultaneous activation of all concepts related to the cat picture (multisensory content: visual representation of the cat picture, a verbal description of the cat picture, and long-term representations of cat related concepts). Examining under what circumstances different content representations are active and what limits, if any, the number of representations that can be active at one time can help us achieve a unified working memory model.

Current working memory models can account for the storage of multisensory information in different ways and addressing the above mentioned question can allow us to differentiate between these models. For example, both Baddeley (2000) and Cowan (2001) assume that multisensory information is stored in the form of a limited number of integrated chunks in an amodal format, in the episodic buffer and focus of attention respectively. Although these models have similar assumptions on how multisensory information is maintained, they will generate different predictions on how information enters and exits this amodal maintenance (e.g., information being transferred from modality specific stores or by shifting attention in activated long-term representations).

The integration of information from different sources is an important aspect of working memory and understanding under which specific circumstances information is integrated or not and how this information is represented and maintained is crucial if we are to further our understanding of working memory processes. As a last point, one interesting option is to approach working memory research in light of the predictive coding framework. The predictive coding framework has the potential to explain many of the apparent discrepancies between modality specific and multimodal accounts of working memory, as it explains how working memory representations are composed of both a modality specific component, that is mainly represented in the functional feedback (or anatomical feedforward) representations, while the multimodal representation is mainly carried by the functional feedforward (or antatomical feedback) representation (see Talsma, 2015 for a discussion).

Here we present some important questions raised by the current dissertation that need to be addressed in the future. How can current working memory models explain multisensory interactions and the apparent flexibility with which people can shift between unisensory and multisensory representations? Under which circumstances is working memory performance determined by unisensory or multisensory representations? And lastly, in the audiovisual domain, under which circumstances will audiovisual information facilitate or interfere with working memory performance?

To conclude, the present dissertation has shown that, both information load (feature load and precision) and object load affect working memory performance and that both are represented in working memory separately. Moreover, it has shown that visual and auditory information can interact and integrate to create a complex, multisensory representation. Depending on the context either just the simple modal representation or the complex high-resolution binding of several features at once will become active. We conclude that a deeper understanding of multisensory processes in working memory is needed to further our understanding on how information is encoded, maintained, and manipulated in working memory.

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CHAPTER 7
NEDERLANDSTALIGE SAMENVATTING

Werkgeheugen is onze vaardigheid om gedurende een korte tijd, een beperkte hoeveelheid informatie te onthouden wanneer deze informatie niet meer fysiek aanwezig is. Hoewel deze vaardigheid vrij eenvoudig lijkt, stelt het ons in staat om een breed scala aan complexe taken en activiteiten uit te voeren. Stel je voor dat je op de stoep van een drukke straat staat. Je hebt honger en besluit om een sandwich te kopen bij een winkel aan de overkant van de straat. Om de sandwich te kunnen kopen, moet je de straat oversteken, de winkel ingaan en de sandwich kopen. Voor en tijdens het oversteken van de straat moet je het verkeer om je heen goed in de gaten houden: auto's naderen van links en rechts, en om je heen lopen mensen in alle richtingen doorelkaar. Je kijkt naar links en je ziet een naderende auto, tegelijkertijd hoor je de sirene van een van rechts naderende ambulance. Op dit moment ben je een aantal dingen actief aan het bijhouden: de naderende auto van links, de naderende ambulance van rechts, je doel om de sandwich te kopen, en het plan om de straat over te steken en de winkel binnen te gaan. Het is niet moeilijk om te zien hoe een falen van het werkgeheugen kan leiden tot problemen in het dagelijkse leven. Het is dan ook geen verrassing dat het werkgeheugen, en de bijbehorende processen, op de voorgrond staat van het onderzoek naar menselijke cognitie.

De informatie die wij onthouden in het werkgeheugen komt uit een grote verscheidenheid aan bronnen: zintuiglijke informatie (bv., de visueel waarneembare auto of auditief waargenomen ambulance), motorische en actie informatie (bv., de geplande actie om de straat over te steken), en het lange-termijn geheugen (bv., de begrippen "straat", "auto", "ambulance" en "bakker"). Dus naast het kort onthouden van informatie, is de integratie van informatie uit de verschillende, bovengenoemde bronnen een belangrijk aspect van het werkgeheugen.

Ondanks het belang van de integratie van informatie uit verschillende bronnen heeft onderzoek in het werkgeheugen veld zich vooral gericht op het onthouden van informatie uit een enkele bron. Hoe informatie wordt geïntegreerd en gerepresenteerd wordt in het werkgeheugen is het centrale thema van dit proefschrift. Het eerste deel van het huidige proefschrift (hoofdstuk 2 en 3) onderzoekt hoe visuele informatie wordt geïntegreerd en gerepresenteerd in het werkgeheugen. Het tweede deel (hoofdstuk 4 en 5) onderzoekt hoe informatie afkomstig van verschillende zintuigen en het lange-termijn geheugen samenkomen en integreren met elkaar.

VISUEEL WERKGEHEUGEN

Een langlopende discussie in het onderzoek naar visueel werkgeheugen heeft betrekking op de vraag hoe visuele informatie precies wordt onthouden in het werkgeheugen. Sommige onderzoekers hebben aangetoond dat visuele informatie die bij elkaar hoort wordt samen gevoegd in de vorm van een aantal visuele objecten. Volgens deze onderzoekers wordt het visueel werkgeheugen beperkt door een vast aantal van deze geïntegreerde objecten die gelijktijdig in het werkgeheugen vast gehouden kunnen worden (Object-gelimiteerd werkgeheugen; zie voor een overzicht:

Luck & Vogel, 2013). Andere onderzoekers hebben aangetoond dat visuele kenmerken van objecten (bv., de kleur of vorm) onafhankelijk van elkaar onthouden kunnen worden en dat deze informatie dus niet noodzakelijk wordt geïntegreerd in een enkel object. Deze laatste groep onderzoekers stellen dat het visueel werkgeheugen niet wordt beperkt door een vast aantal objecten dat onthouden kan worden, maar door de totale aangeboden visuele informatie (Informatie-gelimiteerd werkgeheugen; zie voor een overzicht: Ma, Husain, & Bays, 2014). Een assumptie die voortkomt uit de laatste stelling is dat het aantal objecten dat tegelijkertijd onthouden kan worden in het visueel werkgeheugen afhangt van de precisie waarmee deze objecten verwerkt worden.

In hoofdstuk 2 hebben we onderzocht of visuele objecten in het werkgeheugen verwerkt kunnen worden op verschillende niveaus van detail. We deden dit door gebruik te maken van een veranderings-detectie taak waarbij proefpersonen werden geïnstrueerd om dezelfde visuele figuren te onthouden met verschillende niveaus van detail. Zo konden ze geïnstrueerd worden om enkel de vorm van figuur te onthouden, of bijvoorbeeld, de vorm en de kleur van object te onthouden. De belangrijkste bevinding van deze studie was dat de capaciteit van het visueel werkgeheugen aanzienlijk werd beïnvloed door de hoeveelheid detail die onthouden moest worden per figuur. De nauwkeurigheid waarmee proefpersonen een verandering konden detecteren daalde niet alleen door het aantal objecten dat onthouden moest worden, maar ook door de hoeveelheid detail die onthouden moest worden per figuur. We vonden geen interactie tussen het aantal figuren en de hoeveelheid detail die verwerkt moest worden, wat suggereert dat deze factoren onafhankelijk van elkaar opereren. De resultaten van dit experiment impliceren dat het onthouden van meer detail per figuur ten koste gaat van het aantal figuren dat onthouden kan worden. Bovendien geven onze resultaten aan dat proefpersonen, tot op zekere hoogte, strategisch konden bepalen hoeveel detail ze onthielden per object, afhankelijk van de taakinstructie. Hoewel we voorzichtig moeten zijn met de interpretatie, om redenen die hieronder uiteengezet zullen worden, zijn deze resultaten compatibel met informatie-gelimiteerde modellen van werkgeheugen capaciteit.

Een beperking van de studie in hoofdstuk 2 is dat de drie verschillende niveaus van detail elkaar wederzijds konden beïnvloeden. Zo bracht een verandering in het laagste niveau van detail, de algemene vorm van de figuur, ook een verandering teweeg in het hoogste niveau van detail, de interne ruimtelijke structuur van het figuur. Om dit probleem te omzeilen bedachten we een nieuw experiment met nieuwe stimuli waarbij de visuele kenmerken van de figuur (bv., de vorm of kleur) onafhankelijk gemanipuleerd konden worden. Door deze aanpak konden we deelnemers instrueren om selectief één of meer van deze visuele kenmerken per object te onthouden. Bovendien konden wij op deze manier onderzoeken of de visuele kenmerken van een figuur afzonderlijk in het werkgeheugen vertegenwoordigd zijn, of dat ze met elkaar verbonden worden in een enkele, geïntegreerde object voorstelling.

In hoofdstuk 3 onderzochten we of de visuele kenmerken van een figuur onafhankelijk van elkaar worden onthouden, of dat deze worden onthouden als een geïntegreerde representatie in het visueel werkgeheugen. Daarnaast wilden wij de impact van visuele kenmerken op posterieure hersen activiteit onderzoeken met behulp van elektro-encefalografie (EEG).

In twee experimenten vonden we dat het aantal visuele kenmerken dat per object onthouden moest worden een significante impact heeft op de capaciteit van het visueel werkgeheugen. Het onthouden van meerdere visuele kenmerken per figuur ging ten koste van het totaal aantal figuren dat onthouden kon worden. Ook vonden we een mogelijke dissociatie tussen bilaterale en gelateralizeerde EEG activiteit tijdens het onthouden van figuren met meerdere visuele kenmerken. Bilaterale activiteit nam af in amplitude wanneer meer kenmerken onthouden moesten worden, terwijl gelateralizeerde EEG activiteit toenam in amplitude wanneer er meer figuren onthouden moesten worden, maar enkel aan de contralaterale zijde. Samen met de eerder genoemde gedrags-resultaten suggereren deze bevindingen dat zowel objectinformatie alsmede de visuele kenmerken per figuur afzonderlijk worden gerepresenteerd in het werkgeheugen.

Kortom, de studies in hoofdstuk 2 en 3 tonen aan dat zowel de individuele kenmerken van een figuur alsmede het totaal aantal figuren dat onthouden moet worden het visueel werkgeheugen beperken. Als eerste, geheugen capaciteit voor dezelfde voorwerpen, zoals gemeten met Cowan's *K*, neemt af wanneer het aantal kenmerken of de nauwkeurigheid waarmee figuren onthouden moeten worden wordt verhoogd. Ten tweede, in beide studies nam de prestatie van proefpersonen af met een toename in zowel het aantal figuren alsmede de totale visuele informatie (precisie of kenmerken) die onthouden moest worden. Ten derde, onze EEG resultaten wijzen op een scheiding in de posterieure hersenactiviteit tussen de bilaterale activiteit, die een effect van de totale visuele informatie in geheugen laat zien, en de gelateralizeerde activiteit, die een effect van het totaal aantal figuren in geheugen laat zien. Als laatste, de prestatie van deelnemers nam af wanneer zij werden geïnstrueerd om meer informatie (precisie en kenmerken) te onthouden, dit suggereert dat ze in staat waren om strategisch te bepalen hoe visuele informatie werd gecodeerd, onderhouden en / of opgehaald werd in het werkgeheugen.

Op basis van onze eigen bevindingen en in overeenstemming met recente studies (bv., Fougnie et al, 2010; Fougnie et al, 2016; Vergauwe & Cowan, 2015; Xu & Chun, 2006), gaan we ervan uit dat zowel een object representatie alsmede een kenmerken representatie afzonderlijk worden onthouden in het werkgeheugen (Fougnie et al, 2010; Xu & Chun, 2006). Bovendien gaan we ervan uit dat mensen strategische controle kunnen uitoefenen over hoe visuele informatie wordt gecodeerd en onthouden (Fougnie et al., 2016), en opgehaald (Vergauwe & Cowan, 2015).

MULTISENSORISCH WERKGEHEUGEN

Recente ontwikkelingen op het gebied van multisensorische verwerking hebben het klassieke idee dat wergeheugen representaties modaliteitsspecifiek zijn, in twijfel getrokken (Ghazanfar & Schroeder, 2006). Zo bestaan er bijvoorbeeld zeer snelle interacties tussen de verschillende sensorische systemen (bv., Giard & Péronnet 1999; Talsma, Doty, & Woldorff, 2007), directe verbindingen tussen de visuele en auditieve cortex (bv., Beer, Plank, en Greenlee, 2011; Falchier, Clavagnier, Barone, & Kennedy, 2002), en vroege multisensorische interacties die invloed uitoefenen op het oriënteren van aandacht en geheugenopslag (bv., Van der Burg, Talsma, Olivers, Hickey & Theeuwes, 2011; Talsma, Senkowski, Soto-Faraco, & Woldorff, 2010). Ook hebben een beperkt aantal studies aangetoond dat multisensorische verwerking van invloed kan zijn op de prestaties van het visueel werkgeheugen. Botta et al. (2011) toonde bijvoorbeeld aan dat multisensorische aanwijzingen effectiever zijn bij het sturen van selectie in visueel werkgeheugen dan pure visuele aanwijzingen waren. Ook is gevonden dat geheugencapaciteit voor bimodale stimuli groter is dan die van enkel visuele of auditieve stimuli (bijvoorbeeld Delogu, Raffone & Belardinelli, 2009). Verdere aanwijzingen dat werkgeheugen niet geheel modaliteit specifiek is werden onlangs gevonden door Senkowski, Schneider, Tandler, en Engel (2009), die aantoonden dat de binding van visuele en auditieve kenmerken van een opgeslagen object tot oscillaties van hoge frequentie (> 40 hz) in het EEG vertonen. Tezamen resulteren deze studies in een aanzienlijke hoeveelheid bewijs dat niet-visuele processen een invloed kunnen uitoefenen op visueel werkgeheugen processen. Het blijft echter nog een vraag hoe modaliteitsspecifieke informatie en meer abstracte, contextuele vormen van informatie samenkomen in het werkgeheugen.

In hoofdstuk 4 en 5 hebben wij een poging gedaan om die vraag te beantwoorden. In hoofdstuk 4 hebben we ons gericht op de vraag of een irrelevant auditieve context de ruimtelijke codering kan beïnvloeden waarmee serieel gepresenteerde visuele items zijn vertegenwoordigd in het werkgeheugen en of dit vervolgens werkgeheugen prestatie kan verbeteren. Proefpersonen kregen de opdracht om visueel gepresenteerde Chinese karakters te onthouden in een Sternberg geheugentaak. We hebben drie verschillende auditieve contexten gecreëerd: een monotone, een opgaande en een willekeurige auditieve context. Elk Chinees karakter in de reeks werd gelijktijdig gepresenteerd met één van de vier auditieve tonen. De toon die werd gepresenteerd op een moment in de seriële orde werd bepaald door de auditieve context. We vonden dat de ruimtelijke hercodering van Chinese karakters in seriële orde kan worden beïnvloed door een irrelevant auditieve context. We vonden dat de respons van proefpersonen werd beïnvloed door de ordinale positie van een karakter in de reeks, maar alleen wanneer deze karakters samen werden gepresenteerd met een oplopende auditieve tonenreeks. We concluderen dat de ruimtelijke her-codering van visueel gepresenteerde figuren enkel gebeurd wanneer de auditieve context bestaat uit informatieve en voorspelbare tonen. Alhoewel de informatieve en voorspelbare auditieve context de ruimtelijke codering beïnvloede zorgde dit niet voor een verbetering van geheugen prestaties.

Tenslotte wordt in hoofdstuk 5 de literatuur over audio-visuele interacties en integratie in het werkgeheugen en aandacht besproken. Ondanks dat onderzoek in het verleden heeft gepleit voor modaliteit-specifieke werkgeheugen systemen (bv., Baddeley en Hitch, 1974), bespreken we in hoofdstuk 4 een toenemende hoeveelheid literatuur die suggereert dat cross-modale interacties een belangrijke rol spelen in het werkgeheugen. Studies naar audiovisueel werkgeheugen hebben bijvoorbeeld aangetoond dat: a) recall beter is voor audiovisuele objecten dan voor enkel auditieve- of visuele objecten (Delogu, Raffone, & Belardinelli, 2009 Goolkasian en Foos, 2005; Thompson en Paivio, 1994); b) werkgeheugencapaciteit hoger is voor audiovisuele objecten (Fougnie en Marois, 2011; Saults en Cowan 2007) en c), dat visuele en auditieve informatie kunnen interfereren met elkaar in werkgeheugen (Goolkasian en Foos, 2005; Morey en Cowan, 2004, 2005). Bovendien wordt het memoriseren van modaliteit-specifieke objecten beïnvloed door cross-modale cues (Botta et al., 2011) en wordt modaliteitsspecifieke object discriminatie beïnvloed door een multi-sensorische geheugenrepresentatie (bv., Murray et al., 2004). Deze studies geven aan dat de representaties in het geheugen unisensorisch of multisensorisch kunnen zijn, en dat zowel top-down en bottom-up processen een belangrijke rol spelen bij de integratie van informatie. Op basis van de bovenstaande bevindingen, recente ontwikkelingen in neurowetenschappelijke modellen van het werkgeheugen (D'Esposito & Postle, 2014; Postle, 2006) en de populariteit van het *predictive coding* kader (Friston, 2010), concluderen wij dat een complexe multi-sensorische representatie wordt gecreëerd in het werkgeheugen, die bestaat uit de integratie van verschillende onafhankelijke representaties. Concreet gaan we ervan uit dat de sensorische cortices kleine hoeveelheden unisensorische informatie vast houden (cf. Postle, 2006) en dat deze informatie een multi-sensorische representatie in hogere orde hersen gebieden ondersteunt (Postle, 2006; Yonelinas, 2013).

Tot slot, het huidige proefschrift heeft aangetoond dat zowel totale visueel informatie (visuele kenmerken en precisie) en het aantal geïntegreerde objecten een invloed hebben op werkgeheugen prestaties en dat beide onafhankelijk van elkaar worden gerepresenteerd in het werkgeheugen. Bovendien hebben we aangetoond dat visuele en auditieve informatie samen kunnen komen en integreren om een complexe, multi-sensorische representatie te creëren. Afhankelijk van de context wordt enkel de eenvoudige modale representatie of de complexe binding van verschillende kenmerken tegelijk actief. We concluderen dat een dieper begrip van multi-sensorische processen in het werkgeheugen nodig is om onze kennis over de manier waarop informatie wordt gecodeerd, onderhouden en gemanipuleerd in het werkgeheugen te bevorderen.

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DATA STORAGE FACT SHEETS

In compliance with the UGent standard for research accountability, transparacy and reproducibility, the location of the datasets used in this dissertation are added below. For each of the empirical chapters (i.e., chapters 2 to 4) a separate Data Storage Fact Sheet is completed, detailing which data and analysis files are stored, where they are stored, who has access to the files and who can be contacted in order to request access to the files. In addition, the Data Storage Fact Sheets have been added to my public UGent Biblio account.

DATA STORAGE FACT SHEET FOR CHAPTER 2

Name/identifier study
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Date: 05-12-2016

1. Contact details

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2. Information about the datasets to which this sheet applies

- Reference of the publication in which the datasets are reported:

  Chapter 2 of PhD dissertation (first empirical chapter): Visual working memory varies with increased encoding detail of complex objects

- Which datasets in that publication does this sheet apply to?:

  All data from the reported experiment (behavioral).

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  - [ ] other (specify): ...

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  - [x] all members of the research group
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  - [ ] file(s) containing processed data. Specify: ...
  - [x] file(s) containing analyses. Specify: SPSS scripts (containing all processing steps and their justification)
  - [x] files(s) containing information about informed consent (printed informed consents stored in folder)
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- Reference of the publication in which the datasets are reported:

  Chapter 3 of PhD dissertation (second empirical chapter): Bilateral but not lateralized posterior slow wave activity reflects feature load in visual working memory

- Which datasets in that publication does this sheet apply to?:

  All data from the reported experiment (behavioral + EEG).

3. Information about the files that have been stored

3a. Raw data

- Have the raw data been stored by the main researcher? [x] YES / [ ] NO
  If NO, please justify:

- On which platform are the raw data stored?
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- Who has direct access to the raw data (i.e., without intervention of another person)?
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  - [x] file(s) containing processed data. Specify: Folder with the processed ERP files
  - [x] file(s) containing analyses. Specify: SPSS and MATLAB scripts (containing all processing steps and their justification)
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2. Information about the datasets to which this sheet applies

- Reference of the publication in which the datasets are reported:

  Chapter 4 of PhD dissertation (third empirical chapter): Working memory scaffolding: does auditory context facilitate working memory maintenance. Integration of senses, space, and order in working memory

- Which datasets in that publication does this sheet apply to?:

All data from the reported experiment (behavioral).

3. <u>Information about the files that have been stored</u>

3a. Raw data

- Have the raw data been stored by the main researcher? [x] YES / [ ] NO
  If NO, please justify:

- On which platform are the raw data stored?
  - [x] researcher PC
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- Who has direct access to the raw data (i.e., without intervention of another person)?
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- Which other files have been stored?
  - [ ] file(s) describing the transition from raw data to reported results. Specify:
  - [ ] file(s) containing processed data. Specify:
  - [x] file(s) containing analyses. Specify: SPSS scripts (containing all processing steps and their justification)
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