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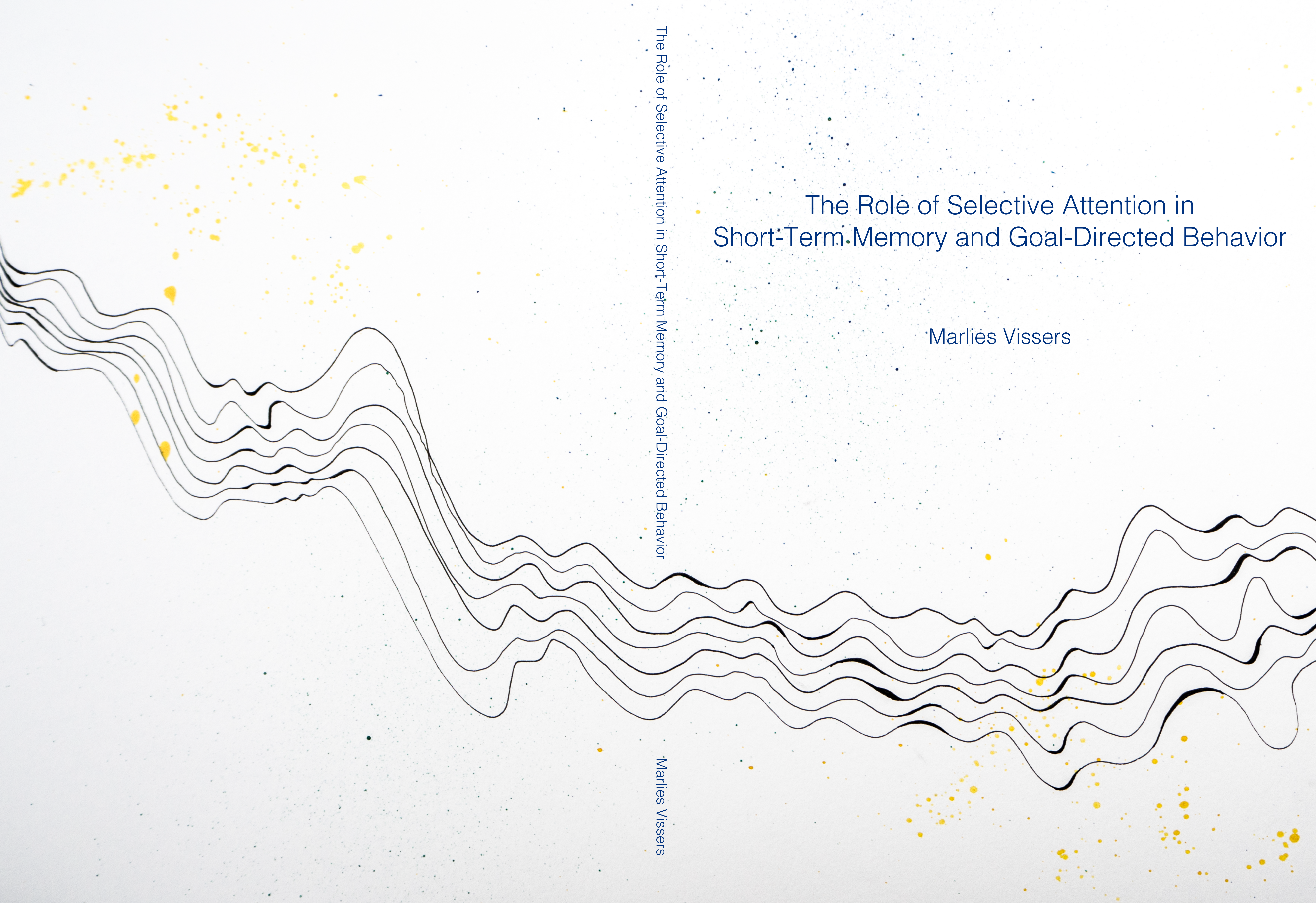

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The Role of Selective Attention in Short-Term Memory and Goal-Directed Behavior

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Faculteit der Maatschappij- en Gedragswetenschappen

CONTENTS

CHAPTER 1

Introduction

Our behavior in everyday life is not just guided by the information that reaches our eyes. Instead, most of our actions rely on internal representations of the outside world. Such internal representations are highly useful in two ways. First, they provide access to information that may change during the course of an action. Second, they may be helpful to prevent an information overload by the rich and cluttered sensory information from the environment, by allowing selective processing and storage of goal-relevant information. Even the simple task of buying a jar of jam in the supermarket for example, requires the ability to form selective representations of the environment. While scanning the shelves, it is essential to be able to remember which flavors were available in order to make a deliberate choice. At the same time, it is efficient to selectively focus on the labels on the jars and not on other aspects of the jars, as only the labels will be helpful to make a choice. This example illustrates how the act of picking a jar of jam in the supermarket, which may feel like a simple task, is not just a result of you reacting on what sensory information, but entails the formation of selective and durable representations of the external world that help to complete an intended behavioral goal.

While the ability to rely on such internal representations may feel natural, our brain performs elegant and sophisticated computations to generate temporarily stable, selective representations of the environment. A key factor that necessitates these cognitive computations is the severe capacity limit of the brain: We can typically only actively process and represent a limited amount of information in a state that is directly accessible for behavioral control. This fundamental capacity limit calls for selective processing of the wealth of sensory information that is continuously presented to our brains.

An important cognitive ability that enables selection and filtering of relevant perceptual information from our environment is selective attention. By filtering of sensory information according to its behavioral relevance, selective attention critically supports the selective formation of internal representations of those aspects of the environment that are relevant to our current goals. These internal representations are useful in preventing information overload, and allow us to keep access to dynamically changing information during the course of an action. In the present thesis, I investigated how selective attention filters visual information to facilitate efficient goal-directed behavior, and the neural mechanisms involved herein.

Selective attention in service of goal-directed behavior

As William James noted more than a century ago, “everyone knows what attention is” (James, 1890). Yet, while the term attention sounds familiar to all of us, attention is a broad term that is used to refer to a range of different processes that also rely on different neural mechanisms. The work in this thesis focuses on selective attention: The ability to selectively process certain goal-relevant visual information from our environment, while ignoring goal-irrelevant sensory information (Gazzaley & Nobre, 2012), and its role in other cognitive abilities in particular the ability to store temporary copies of the environment, and the ability to select an appropriate behavioral response. Furthermore, in the present thesis, I studied how selective attention facilitates goal-directed behavior in the visual domain. This was primarily motivated by previous research revealing useful and robust EEG markers of visual attention, which I employed to measure attentional processes in the context of goal-directed behavior in the present thesis. Although I did not explicitly address similarities between visual selective attention and selective attention in other modalities (e.g., auditory or tactile attention), it is conceivable that the principles that apply to visual selective attention discussed in this thesis, will also apply to selective attention in other modalities.

Selective attention is essential for efficient performance in many everyday life situations in which you need to focus on goal-relevant information while preventing interference from irrelevant events, such as when driving through traffic or when paying attention in school. Notably, not everyone is equally effective at filtering out distraction. Some of us are highly proficient at selectively processing goal-relevant information in distracting conditions, while others are much more easily distracted (Awh, Vogel, & Oh, 2006; Kane & Engle, 2003; Kane, Poole, Tuholski, & Engle, 2006; Luck & Vogel, 2013). The ability to selectively attend to goal-relevant information is a strong predictor of other core cognitive abilities such as visual short-term memory (VSTM) and the execution of goal-directed actions (Kane & Engle, 2003). What is it that the brain should actually do in order to optimally process goal-relevant information to facilitate performance?

One important mechanism through which selective attention can facilitate goal-directed behavior is through top-down modulation of sensory processing. That is, through top-down control, attention can prioritize sensory processing of relevant information at the expense of irrelevant information (Carrasco, 2011; Pinsk, Doniger, & Kastner, 2004; Serences & Yantis, 2006). Yet, the precise ways in which sensory modulations may support the formation of short-term memories or the selection of goal-directed actions remains presently unknown. Does attentional modulation of sensory processing facilitate the formation and maintenance of short-term memories and/or the selection of goal-directed actions? And how are such processes implemented at the neural level?

In the present thesis, I set out to determine how selective attention influences short-term memory and goal-directed action, and investigated the underlying neurophysiological mechanisms. Answers to these questions may further our understanding of how attention supports other core cognitive abilities and may also have clinical relevance: Various neuropsychological conditions are characterized by problems with selective attention and distractibility, including Attention Deficit Hyperactivity Disorder (ADHD; Fassbender et al., 2009), Autism Spectrum Disorder (ASD; Murphy, Foxe, Peters, & Molholm, 2014), and schizophrenia (Gray et al., 2014; Kreither et al., 2017). Furthermore, healthy aging may also be associated with a decline in attentional filtering ability (McNab et al., 2015).

In the following paragraphs, I will first discuss the role of selective attention in VSTM, and in supporting goal-directed actions in the presence of interference. I will then review various ways through which attention may modulate neural processing of sensory information to prioritize processing of relevant information, and the neural mechanisms that allow for attentional modulations at different levels of processing. Lastly, I will briefly introduce the behavioral and electrophysiological measures of selective attention that were used in my thesis research. Hereby, this introduction forms an outline of the background against which the different studies on individual differences in selective attention in the present thesis were conducted.

Selective attention allows for efficient use of short-term memory

The ability to store goal-relevant features of the environment in a format that is directly accessible for control of behavior is essential for everyday activities. This ability is typically called visual short-term memory. There is hardly any task that can be completed without maintenance of information in VSTM. Imagine for example that you need to cross a busy street. You cannot successfully complete this task without being able to remember what you saw on your left, while checking the right side, before crossing the street. By allowing continuous access to perceived representations that disappeared from direct sight or the environment, VSTM enables purposeful behavior in dynamically changing environments. Importantly, however, VTSM is characterized by a severe capacity limit: Our brain can only store a finite and limited amount of information in a state that is readily accessible for behavioral control. VSTM capacity is usually estimated at three to four items (Alvarez & Cavanagh, 2004; Cowan, 2001; Luck & Vogel, 2013; Vogel & Machizawa, 2004). Notably, the precise number of items that can be maintained varies substantially across individuals (Luck & Vogel, 2013).

Given the severe capacity limitation of VSTM, attentional selection of information for representation in VSTM is essential, as this ensures availability of goal-relevant information for behavioral control and prevents needless storage of task-irrelevant items (Awh & Vogel, 2008; Cowan & Morey, 2006; Kane & Engle, 2003). The importance of attentional selection for VSTM performance is supported by studies showing that selective attention is a strong predictor of individual VSTM capacity. For instance, individuals who are better at focusing on goal-relevant information in the presence of distraction or preventing storage of irrelevant information, are generally able to store more information in VSTM compared to individuals who are less proficient at selectively focusing on goal-relevant information (Fukuda & Vogel, 2009; Fiona McNab & Klingberg, 2008; Vogel, McCollough, & Machizawa, 2005). By filtering out task-irrelevant information, selective attention thus fulfills an essential role in supporting VSTM performance.

At the neural level, frontoparietal networks and the basal ganglia have been shown to be important for filtering information that is eventually stored in VSTM (Baier et al., 2010; Fiona McNab & Klingberg, 2008). Yet, it is presently less clear to what extent attentional filtering during VSTM also relies on local modulations of sensory activity. The notion that modulations of sensory activity associated with to-be-encoded representations may underlie efficient short-term memory performance has recently gained popularity. The sensory recruitment hypothesis (Serences, Ester, Vogel, & Awh, 2009) and common source hypothesis (Zelinsky & Bisley, 2015), for example, posit that modulation of sensory activity associated with goal-relevant, to-be-stored information serves as a mechanism underlying VSTM encoding and storage of information. Existing evidence for the involvement and functional role of sensory modulations for selective encoding and storage of information in VSTM is selectively based on findings from studies using low memory loads (one or two greatly distinct items at the same time; Serences, Ester, Vogel, & Awh, 2009b; Towler, Kelly, & Eimer, 2015), or using sequential presentation of multiple items when memory load was higher (Emrich, Riggall, Larocque, & Postle, 2013). Yet, VSTM in everyday life may well concern richer sensory representations that contain multiple to-be-stored items, or even distractors (Orhan & Jacobs, 2014; Peelen & Kastner, 2014). Existing findings thus leave unclear to what extent sensory modulations may also underlie VSTM of multiple simultaneously presented items, and to what extent these also help to suppress distraction during the formation of memories in cluttered visual environments.

A second outstanding question concerns whether attention also helps to protect VSTM content during postperceptual stages of VSTM. Evidence from studies using retrocues to probe attention during postperceptual stages of VSTM indicates that attention continues to affect VSTM contents even during VSTM maintenance. These studies show that the presentation of a retrocue indicating that part of the memory load has become irrelevant for the participants' immediate task results in improved memory for the remaining item, reflecting ongoing attentional selection of VSTM content even after encoding (Griffin & Nobre, 2003; Kuo, Stokes, & Nobre, 2012; Landman, Spekreijse, & Lamme, 2003; Murray, Nobre, & Stokes, 2011). Importantly however, retrocues form explicit cues that signal the need to perform additional attentional selection on VSTM contents during maintenance (Myers, Stokes, & Nobre, 2017). Yet, VSTM in everyday life does not necessarily involve explicit cues that allow you to manipulate the content of VSTM: you sometimes need to store multiple representations in VSTM without being informed only one of the representations will be useful to achieve your goal. This renders it unclear whether typical VSTM maintenance in the absence of external cues similarly relies on attention, and if so, how the role of attention during VSTM maintenance develops changes over time (i.e., is transient or not; Myers, Stokes, & Nobre, 2017).

In the present thesis, I addressed these outstanding questions and examined the role of attention in modulation of sensory activity during VSTM of cluttered and rich visual representations (Chapter 2, 3 and 4), as well as the extent to which the role of attention during VSTM encoding may extend to VSTM maintenance (Chapter 3 and 4).

Selective attention facilitates action selection

Selective attention is not only involved in prioritization of information for short-term storage, but also facilitates the execution of behavioral responses in accordance with given current goals. Many visual events in everyday life are associated with a particular action, such that perceiving it will automatically activate the associated response. Imagine, for example, that you are at working on your computer, trying to finish an article before the deadline that is rapidly approaching. While your goal is to focus and finish your article in time, the sound of your smartphone signaling a new incoming message, may automatically trigger you to pick it up and read the new message, even though doing so will interfere with the goal of finishing your article on time. This illustrates how an automatic association between a sensory stimulus (the sounds of your phone) and a behavioral response (picking up the phone) may facilitate quick and effortless behavior in some situations, but may also interfere with goal-relevant actions.

In situations in which sensory information activates response tendencies that interfere with a behavioral goal, the detection and subsequent resolution of such response conflict is essential to prevent the execution of a response that will lead to a mistake. One way in which one could prevent such a mistake is by quickly inhibiting the automatically activated response, such as the tendency to grab your phone (Aron, 2007). An alternative, not mutually exclusive way to prevent or resolve response conflict is to modulate visual processing so that processing of task-irrelevant information is minimized and that of goal-relevant sensory information is prioritized (Cohen & Ridderinkhof, 2013; Crump & Milliken, 2009; Egner, 2008; Polk, Drake, Jonides, Smith, & Smith, 2008). For example, focusing your attention stronger on your screen instead of the sounds from your environment may prevent you from continuously checking your phone. The idea that attentional modulation of sensory activity is an important means to facilitate goal-relevant behavior is currently growing and is outlined in the notion of sensory priority maps, i.e., topographically organized sensory representations of the environment, that mediate the role of attention in goal-directed behavior (Bisley & Goldberg, 2010; Gottlieb, 2007). Through goal-directed sensory modulations, priority maps may help to bias information processing towards goal-relevant information and prevent irrelevant information from driving actions.

The notion that sensory priority maps facilitate the execution of goal-directed actions implies that modulations of sensory activity should contribute to response selection. Yet, present knowledge on the contribution of sensory processing and modulations hereof to efficient response selection is presently limited. While there is evidence for attenuation of sensory processing of task-irrelevant information upon detection of an error or response conflict (King, Korb, von Cramon, & Ullsperger, 2010; Pastötter, Dreisbach, & Bäuml, 2013), it is presently much less clear whether sensory processing of goal-relevant and goal-irrelevant stimulus dimensions contributes to response selection. For instance, is it the case that the extent to which task-irrelevant information is processed predicts the activation of an incorrect behavioral response? Or is response selection fully dependent on domain-general control mechanisms that detect conflict during response selection? In the present thesis, I set out to determine whether individual differences in attentional modulation of sensory processing affect response selection (Chapter 5).

Characteristics of selective attention during goal-directed behavior

Below I will discuss some important forms and aspects of selective attention that are useful when studyimg how selective attention may facilitate goal-directed behavior.

Location vs. feature-based attention

As you may be able to infer from your own experience, attention can be guided by a variety of stimulus aspects, such as the color, size, shape, or location of items (Wolfe & Horowitz, 2004). For example, imagine driving your car through the city at night, trying to avoid hitting any cyclists that you pass. In order to prevent yourself from having to scan every possible location to check for the presence of a cyclist, it might be easier to focus on the part of the road that is the most likely location for cyclists. Cyclists will usually appear in the lower right of your visual field, and not in the upper half (in the air) or the center of the road (where the cars are driving). Alternatively, you could try to detect any cyclists by focusing on their backlights that will appear as small, red, and moving dots. This example illustrates how spatial and feature-based attention form two common and powerful principles that guide selection of goal-relevant information in visually cluttered environments (Peelen & Kastner, 2014).

Spatial attention enhances visual processing at the attended location, while information in other parts of the visual scene is processed to a much lesser extent or is even suppressed (Saalmann, Pigarev, & Vidyasagar, 2007). The function of spatial attention was initially put forward as a spotlight or zoom lens reflecting continuous enhancement of visual processing at an attended location (Eriksen & St. James, 1986; Eriksen & Yeh, 1985; Posner, Snyder, & Davidson, 1980). Yet, more recent research suggests that the notion of spatial attention as a unifocal zoom lens may be too limited. Attention can be simultaneously allocated across multiple distinct, non-adjacent regions in space (Cavanagh & Alvarez, 2005; Malinowski, Fuchs, & Müller, 2007; Muller, Malinowski, Gruber, & Hillyard, 2003; McMains & Somers, 2004). Moreover, recent sophisticated analyses of the spatiotemporal dynamics of the attentional focus reveal rhythmic alternations between attended locations (Buschman & Kastner, 2015; Fiebelkorn, Saalmann, & Kastner, 2013; Landau & Fries, 2012). Spatial attention can thus be employed to select task-relevant information flexibly and dynamically from the environment, based on current behavioral demands.

Rhythmic alternations of spatial attention between multiple relevant locations have now been replicated across different studies and experimental paradigms (Dugué, McLelland, Lajous, & VanRullen, 2015; Fiebelkorn et al., 2013; Landau & Fries, 2012; Landau, Schreyer, Van Pelt, & Fries, 2015). Possibly, attention also serves to sample or rehearse different representations in a sequential fashion during VSTM encoding and maintenance. According to the attentional rehearsal hypothesis for example, spatial attention rehearses former stimulus locations to maintain VSTM contents in an active and accessible state (Awh, Jonides, & Reuter-Lorenz, 1998; Postle, Awh, Jonides, Smith, & D'Esposito, 2004). Yet, the extent to which attention may sequentially or rhythmically sample and rehearse (to-be-stored) items in VSTM is presently unclear.

While spatial attention helps focusing information processing resources to restricted parts of your visual field, feature-based attention facilitates selection and processing of information based on non-spatial features such as color, shape, or motion direction. Importantly, it affects processing of information throughout the entire visual field, regardless of the location at which the information is presented (Jehee, Brady, & Tong, 2011; Liu, Larsson, & Carrasco, 2007; Maunsell & Treue, 2006; Sàenz, Buraĉas, & Boynton, 2003). Spatial and feature-based attention often take place in parallel (Andersen, Fuchs, & Müller, 2010; Desimone & Duncan, 1995; Egner et al., 2008; Fuchs, Andersen, Gruber, & Müller, 2008), and may interact to facilitate efficient selection of goal-relevant information. Together, they allow for flexible and dynamic selection of goal-relevant information in sensory rich and complex environments.

Although the characteristics of spatial and feature-based attention have been investigated intensively over the past decades, their precise contributions to VSTM or response selection have been studied to a much lesser extent. For example, while converging evidence shows that individuals who are more proficient at attentional filtering make more efficient use of the available storage capacity in VSTM (Luck & Vogel, 2013), knowledge about how such an attentional filter works at the neural level is presently lacking. Does filtering involve suppression of sensory information characterized by task-irrelevant features? Or are features only used to initially select information, after which representations are translated into a spatially organized format such as a priority map? In the present thesis, I used manipulations of spatial as well as feature-based attention to study how selective attention facilitates goal-directed behavior (Chapters 2-5).

Temporal dynamics of selective attention: Proactive (early) vs. reactive (late) attentional filtering

In some situations, one can anticipate the need for attentional control beforehand, while in other situations, attentional control may be unexpectedly called for. An important distinction is thus whether attention can be employed even before the sensory input arrives, or only later upon detection of goal-irrelevant information. These two types of attention are referred to as proactive and reactive attentional control (Geng, 2014).

When the presence and onset of task-irrelevant information is to some extent predictable, proactive attentional control may prevent needless processing of task-irrelevant information through early filtering of goal-irrelevant information (Broadbent, 1966). Early filtering involves fast and rapid extraction of basic physical properties of perceived visual information, after which irrelevant information is instantly prohibited further access to processing resources. Proactive attentional filtering thus leaves as much processing capacity available for goal-relevant information as possible, and is therefore the most effective way to prevent interference by irrelevant sensory information (Geng, 2014).

Yet, our daily environment is volatile and does not always enable anticipation of irrelevant or distracting information. In addition, the continuous implementation of proactive attentional control is likely to be metabolically costly, and may be sensitive to failures when other tasks simultaneously impose cognitive effort (Braver, 2012; Marini, Chelazzi, & Maravita, 2013; Marini, Demeter, Roberts, Chelazzi, & Woldorff, 2016). Proactive suppression of anticipated distraction may thus not always be feasible in everyday life or sufficient to support goal-directed behavior.

Reactive attentional control provides another way to prevent or minimize distractor-related impairments of goal-directed behavior. Reactive attentional filtering entails various cognitive operations, such as detecting the need to filter the irrelevant sensory information (Appelbaum, Smith, Boehler, Chen, & Woldorff, 2011; Marini et al., 2013; Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012), correcting for undesired attentional capture by relocating attention to goal-relevant representations (Braver, 2012; Schwarzkopp, Mayr, & Jost, 2016), and/or suppression or inhibition of further processing of task-irrelevant distractors (Appelbaum et al., 2011; Sauseng et al., 2009). The medial frontal cortex is an important brain region involved in signaling the need for increased control, and the subsequent implementation hereof (Cohen, 2014; Nigbur et al., 2012; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Stankevich & Geng, 2014). At the sensory level, reactive distractor suppression may occur through rapid modulation of processing of task-irrelevant information upon detection of distractors (Appelbaum et al., 2011; Nigbur et al., 2012; Polk et al., 2008; Sauseng et al., 2009). Importantly, however, present knowledge on reactive distractor filtering is still limited compared to knowledge on proactive filtering mechanisms (Geng, 2014). In addition, the difference between the roles of proactive vs. reactive filtering for accurate VSTM performance has presently received little attention. Research on the neural principles through which rapid, reactive modulations of sensory activity may help to minimize the effect of unanticipated distraction during VSTM or response selection is thus essential. The research described in chapter 2 and 5 of this thesis was designed to study proactive as well as reactive distractor filtering during VSTM and response selection, and the neural mechanisms involved.

Neural principles of selective visual processing

Attention facilitates goal-directed behavior by biasing sensory processing towards goal-relevant visual information, at the expense of irrelevant information. At the neural level, this effect may be implemented through different neural principles such as response gain, noise suppression, and biased competition (Chelazzi, Miller, Duncan, & Desimone, 1993; Kastner & Ungerleider, 2001; Reynolds & Heeger, 2009; Roelfsema, Lamme, & Spekreijse, 1998). At the population level, attentional modulation of sensory processing is typically categorized as enhancement of goal-relevant information, versus suppression or inhibition of goal-irrelevant information (Gazzaley & Nobre, 2012; Geng, 2014), reflecting two different mechanisms through which goal-relevant information can be prioritized for behavioral control. Yet, present knowledge on the differential roles of enhancement versus suppression of information during selective attention in the context of goal-directed behavior is limited.

Various studies demonstrate goal-directed modulation of sensory processing during VSTM or response selection as a result of selective enhancement of goal-relevant information processing (Egner & Hirsch, 2005; King et al., 2010; Painter, Dux, Travis, & Mattingley, 2014). Other evidence however suggests that distractor suppression is the critical factor predictive of efficient goal-directed performance (Gaspar, Christie, Prime, Jolicœur, & McDonald, 2016; Gulbinaite, Johnson, de Jong, Morey, & van Rijn, 2014; Fiona McNab & Klingberg, 2008; Vogel et al., 2005; Zanto & Gazzaley, 2009). Yet another line of research shows that prioritization of goal-relevant information is not the result of selective enhancement or suppression of goal-relevant or distracting information respectively, but is a product of biased competition between different competing representations, such that enhanced processing of a relevant stimulus dimension is inherently accompanied by decreased processing of the task-irrelevant dimension (Polk et al., 2008; Snyder & Foxe, 2010). Clearly, there is presently no consensus regarding the involvement and functional importance of attentional enhancement or suppression of relevant and distracting information during VSTM or response selection. Furthermore, the extent to which these processes occur as ongoing attentional modulations, or instead reflect transient adjustments, is presently unknown. The extent to which enhancement of goal-relevant information, suppression of goal-irrelevant information, or the combination of both, explain the effect of selective attention on VTSM and response selection, was assessed in chapter 4 and 5 of this thesis.

Measuring selective attention in service of goal-related behavior

Behavioral measures of selective attention

In laboratory settings, selective attention in service of VTSM is typically investigated with computer tasks such as the change-detection task (Figure 1). In a change-detection task participants are briefly presented with a display that contains multiple items. These memory items are usually simple geometric shapes of which participants need to remember a particular feature, such as their color (see Figure 1a). After a delay period of one to two seconds, the accuracy of the participants' memory representation is probed by a display that contains a probe at the position of one of the memory items. The participant is then asked to indicate whether the probe item is identical to the stimulus at that position in the initial memory display. Change detection tasks can be used to quantify VSTM capacity (Luck & Vogel, 1997; Rouder, Morey, Morey, & Cowan, 2011; Vogel, Woodman, & Luck, 2001), which is computed as the maximal number of items (K) that can be stored accurately in memory (K_{max}; Cowan, 2001; Pashler, 1988).Importantly, change-detection tasks have also been used to simulate situations that contain distraction by introducing task-irrelevant stimuli (distractors) in the memory display. Figure 1b shows an example of a stimulus display with distractors, in which stimulus shape differentiates between targets (circles) and distractors (squares). Manipulation of the number of distractors in the memory display (see Figure 1b) forms an important means to assess the effect of distractors on behavior and/or neural activity (Fukuda & Vogel, 2009; Vogel et al., 2005). When memory performance, or neural activity reflecting storage of information in VSTM, changes as a function of the number of distractors, this indicates that participants could not entirely prevent distractors from entering VSTM. Change-detection tasks can thus be employed to

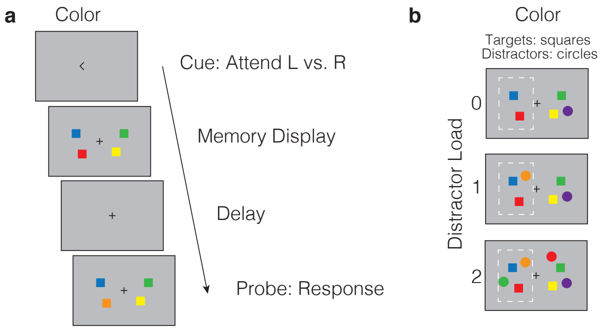

Figure 1. Change detection tasks can be used to measure visual short-term memory capacity and distractor filtering. A) Graphical display of a trial in a change detection task. In this example, the memory display contains goal-relevant items only (load 2). Participants are asked to remember the color of the target stimuli (squares). B) Illustration of an adaptation of a change detection task that also contains distractors (circles). Comparing performance in the presence and absence of distraction, while keeping memory load constant, reveals how well participants can suppress distraction during VSTM.

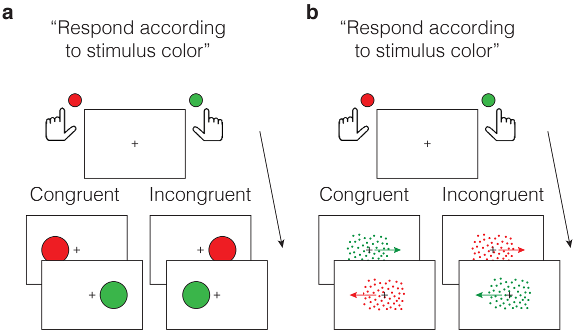

Figure 2. Simon tasks measure response conflict as a consequence of interference by goal-irrelevant stimulus dimensions. A) A classical variant of a Simon task, in which participants are asked to respond to the color of the stimulus (using their left hand for red and their right hand green). On congruent trials, the stimulus appears on the side corresponding to the hand that should be used to respond. On incongruent trials, the stimulus appears on the other side of the screen. Performance on incongruent trials is typically impaired, reflecting response conflict. B) A modified version of the Simon task in which participants perceive colored moving dot patterns. Participants are asked to respond to the color of the stimulus (using their left hand for red and their right hand for green). On congruent trials, the dot pattern moves in the direction corresponding to the hand that should be used to respond. On incongruent trials, the pattern moves in the opposite direction, resulting in response conflict.

assess VTSM capacity as well as attentional filtering in service of short-term memory (Luck & Vogel, 2013). In chapters 2, 3 and 4, I used different versions of the change detection task to assess the role of attention in VSTM.

Response conflict elicited by goal-irrelevant information can be investigated using a Simon task (Lu & Proctor, 1995; Simon & Wolf, 1963). In a typical Simon task, participants are presented with a display that shows one of two stimuli associated with a response (left or right button press) presented at the side of the screen corresponding to the response hand (congruent trials) or at the other side of the screen (incongruent trials). For example, participants are asked to respond to a green circle with their left hand, and to respond to a red circle with their right hand, regardless of the side of presentation (see Figure 2a). When performing such a task, it is much easier to respond correctly if the stimulus is presented on the side of the screen corresponding to the hand that is required for a correct response, compared to when the stimulus is presented on the other side. Accurate performance on incongruent trials thus requires selective inhibition of the response activated by the irrelevant stimulus location to allow execution of the goal-relevant and correct response to stimulus color (Ridderinkhof, Forstmann, Wylie, Burle, & van den Wildenberg, 2011). Response incongruence (response conflict) is associated with increased response times and error rates. Quantification of the size of the behavioral and neural conflict effect yields insights into the degree to which task-irrelevant information can be prevented from interfering with goal-directed behavior. In chapter 5, I used a modified version of a Simon task, in which response conflict could be elicited by motion direction or stimulus color (see Figure 2b), to examine individual differences in response conflict elicited by different visual features.

Individual differences in memory performance and/or behavioral distractor costs provide an important source of information regarding the functional role of attentional filtering for other cognitive abilities (Vogel & Awh, 2008). In chapters 3, 4 and 5 of this thesis I therefore adopted an individual differences approach to further understanding of the functional role of selective visual attention in goal-directed behavior, and the neural mechanisms involved.

Electrophysiological measures of selective attention

In order to obtain a better understanding of how the brain prioritizes goal-relevant over goal-irrelevant processing in service of VSTM and response selection, I used electrophysiology (EEG) to investigate patterns of brain activity involved in selective attention during VSTM and action selection. Below I provide a brief overview of the different electrophysiological markers that are associated with selective attention and will be used in the current thesis. These measures can be broadly categorized as measures of attentional modulation of sensory processing, the efficiency of attentional filtering, and lastly, measures signaling the need to filter or resolve conflict.

Local power modulations of alpha oscillations

Electrophysiological brain activity is rhythmic in nature: brain signals continuously wax and wane in a periodic manner. The rhythms observed in the brain range between slow oscillations at frequencies in the range of ± 1 Hz, to faster activity in the range of 40-100 Hz (Fries, 2015). One particularly important rhythm supporting selective attention is the alpha rhythm (Klimesch, 2012). Alpha oscillations reflect rhythmic electrophysiological activity in the frequency range between 8-12 Hz that is strongest in sensory and somatosensory cortices, and can even be detected in the raw EEG trace (Adrian & Matthews, 1934). The oscillatory nature of alpha activity is thought to reflect rhythmic fluctuations in (phasic) inhibition of local neuronal excitability (Jensen & Mazaheri, 2010; Klimesch, 2012; Klimesch, Sauseng, & Hanslmayr, 2007). These rhythmic pulses of inhibition exert more powerful effects when the signal is stronger: Increased alpha power in a particular region results in enhanced inhibition of sensory processing, while decreased alpha power within a particular area reflects a release of inhibition, allowing for increased sensory processing. According to this perspective, alpha oscillations thus form a mechanism through which information processing can be coordinated both at the network level, by routing information processing to task-relevant regions, but also at the local level, through rhythmic inhibition of sensory processing.

Power of alpha activity can be modulated locally under top-down control, and thereby forms a flexible means to prioritize processing of information in goal-relevant versus goal-irrelevant brain regions (Jensen, Gips, Bergmann, & Bonnefond, 2014; Jensen & Mazaheri, 2010; Figure 3a). Alpha power modulations facilitate spatial (Kelly, Lalor, Reilly, & Foxe, 2006; Rihs, Michel, & Thut, 2007; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden, Foxe, Wang, & Simpson, 2000) as well as feature-based attention (Romei, Thut, Mok, Schyns, & Driver, 2012; Snyder & Foxe, 2010; Volberg, Kliegl, Hanslmayr, & Greenlee, 2009). Furthermore, while most evidence on the involvement of alpha power modulations in selective attention concerns proactive alpha power modulations during anticipated distraction, alpha power modulations may also be involved in suppression of unanticipated distractor load during VSTM in a distractor load-dependent way (Sauseng et al., 2009). Local alpha modulations are thus a highly flexible and important neural mechanism involved in the modulation of sensory processing, and form a powerful way in which various different types of attention may be implemented in the brain.

Beyond the single study on the role of alpha power modulations in distractor suppression during VSTM encoding and maintenance (Sauseng et al., 2009), knowledge on the role of alpha power modulations for distractor suppression during VSTM is limited (Gazzaley & Nobre, 2012). For example, whether their involvement in proactive distractor suppression extends to more reactive situations, and the extent to which these mechanisms scale with distractor load remains presently unclear. In Chapter 2 of the present thesis, I tested the distractor load-dependence of occipital alpha power modulations during proactive as well as reactive distractor suppression during encoding and maintenance of information in VSTM. Analyses of alpha power modulations were complemented by ERP measures reflecting the need to filter distractors during VSTM (Liesefeld, Liesefeld, & Zimmer, 2014), and ERP measures of the amount of (irrelevant) information stored in VSTM: the contralateral delay activity (CDA; Vogel et al., 2005; see Figure 3b), which forms a measure to quantify the effect of attentional filtering on behavior.

Steady state visual evoked potentials

Steady state visual evoked potentials (SSVEPs) provide us with another effective tool to assess attentional modulation of visual processing. SSVEPs are evoked responses elicited by flickering stimuli that periodically change contrast or luminance, resulting in a periodic electrophysiological response at the exact same frequency as the flickering stimulus (Norcia, Appelbaum, Ales, Cottereau, & Rossion, 2015; Vialatte, Maurice, Dauwels, & Cichocki, 2010; see Figure 3c). An important feature of SSVEPs is that

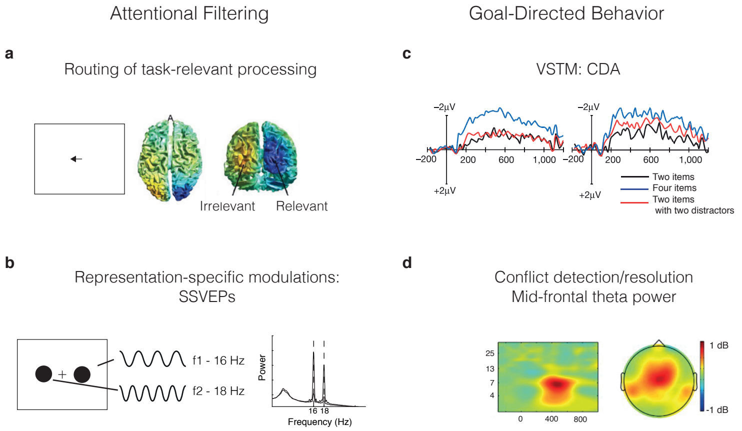

Figure 3. Overview of electrophysiological measures used to investigate attentional filtering in the present thesis. A) Illustration of attentional modulation of local alpha power in task-relevant and task-irrelevant cortices. While participants attend to the left side of the screen, alpha power in visual cortex in the hemisphere processing the attended side of the screen is suppressed (blue colors), while alpha power in the hemisphere processing the unattended side of the screen is increased (red colors). Adapted from Zumer, Scheeringa, Schoffelen, Norris, & Jensen (2014). B) Illustration of how the memory load-sensitivity of the contralateral delay activity (CDA) can be used to assess the extent to which participants can filter distraction. When the amplitude of the CDA for a trial with 2 targets and 2 distractors (red trace) resembles the amplitude on trials with 4 targets (blue trace), this suggests that participants encoded distractors into VSTM similar to the target stimuli. Contrarily, if CDA amplitude for a trial with 2 targets and 2 distractors resembles the amplitude on trials with 2 targets (black trace), this suggests participants selectively encoded target stimuli into VSTM, and perfectly filtered out the distractors. Adapted from Vogel et al. (2005). C) Illustration of the use of Steady-State Visual Evoked Potentials (SSVEPs) to simultaneously track how attention may modulate sensory representations of multiple stimuli. By frequency tagging different stimuli with distinct frequencies, it is possible to investigate attentional modulations of multiple individual stimulus representations at the same time. D) Example of a conflict-related mid-frontal theta response, centered at FCz. The left panel shows the time-frequency representation of conflict-related oscillatory activity. Here, the x-axis represents time, while the y-axis represents frequencies. The oscillatory response is phasic and restricted to the theta frequency band (4-8 Hz). The right panel shows a topographical display of conflict-related theta activity and shows that the effect is centered at mid-frontal sites (electrode FCz). Adapted from Cohen (2014).

their amplitude is enhanced by attention (Andersen et al., 2010; Malinowski et al., 2007; Muller, Bartelt, Donner, Villringer, & Brandt, 2003). SSVEP responses have been shown to be increase with spatial (Malinowski et al., 2007; Muller et al., 2003) as well as feature-based attention (Andersen, Hillyard, & Müller, 2008; Garcia, Srinivasan, & Serences, 2013), providing a useful method to continuously track visual attention to a given stimulus or location. Moreover, using the precise and known frequency response of SSVEPs, attentional allocation to multiple representations can be tracked simultaneously, by using individual frequency tags for different representations or locations (Itthipuripat, Garcia, & Serences, 2013; Toffanin, de Jong, Johnson, & Martens, 2009). Importantly, SSVEPs enable tracking of attention without the need to introduce additional attentional cues into the task, such as retrocues for example, and as such, provide an ideal tool for studying the role of attention in VSTM. In chapter 3 and 4 of this thesis, I used SSVEPs to examine the spatiotemporal dynamics of attentional deployment to individual stimulus representations throughout VSTM encoding and maintenance in the absence of external cues, and examined if individual differences herein predicted VSTM performance.

Neural measures reflecting the detection and resolution of conflict

When task irrelevant information is not filtered efficiently, it may interfere with goal-relevant actions, and/or trigger an inappropriate behavioral response. The detection and implementation of the need for increased cognitive control is typically accompanied by a transient increase in theta power (~ 6 Hz) over midfrontal scalp sites (Cavanagh & Frank, 2014; Cohen, 2014). Mid-frontal theta oscillations serve a general function in conflict detection and/or resolution, and have been observed during stimulus as well as response conflict (Cohen & Ridderinkhof, 2013; Nigbur, Ivanova, & Stürmer, 2011).

While mid-frontal theta oscillations play an important role in the detection of the need for increased attentional control, the implementation of increased attentional control requires interregional communication. An important mechanism underlying interregional communication is phase synchronization of oscillatory activity (Fries, 2015). When oscillatory activity across distant neural populations becomes temporally aligned in terms of its oscillatory phase, this phase alignment (phase connectivity) is thought to provide a 'temporal code' or 'window of communication' through which neural activity at distant cortical regions becomes coupled over time (Engel, Gerloff, Hilgetag, & Nolte, 2013; Fries, 2005). Such interregional coupling enables interregional transmission of information across distant regions in the brain.

Two particularly important frequency bands involved in interregional communication subserving attention and cognitive control are alpha and theta band interregional synchronization. Frontoparietal alpha synchronization has been shown to be important for selective attention and working memory (Palva & Palva, 2007, 2011). Theta band synchronization between mid-frontal and other task-relevant sites on the other hand, has been shown to be important for conflict resolution during and following response conflict (Cohen, 2014; Nigbur et al., 2011). The extent to which these different oscillatory mechanisms may be involved in attentional modulations directed at the resolution of response conflict is presently unknown. In chapter 5, I examined if the extent to which attentional modulation of feature-specific sensory processing (as reflected in interregional communication by means of alpha and theta phase synchronization between midfrontal cortex and sensory regions) may help to reduce response conflict induced by a task-irrelevant visual feature.

Thesis Outline

In this thesis, I investigated how selective attention supports VSTM capacity and the ability to select goal-relevant actions. In addition, to gain a better understanding of how the brain may help us to overcome distraction, I examined the presence and characteristics of electrophysiological correlates of attentional filtering during VSTM and response selection. In chapter 2, I investigated proactive and reactive distractor filtering during VSTM. Specifically, in order to establish whether alpha activity is specifically involved in distractor suppression in the context of VSTM, I investigated whether occipital alpha power scales with the number of distractors. In the subsequent chapters, I aimed to shed more light on the extent to which VSTM performance relies on representation-specific modulations of sensory activity. These studies were aimed to investigate if attention continues to protect stored representations in VSTM during postperceptual stages of VSTM in the presence (chapter 4) and absence (chapter 3) of distraction. Here, I also examined the temporal dynamics of attention during VSTM encoding and maintenance. Specifically, in chapter 3, I tested if attentional modulations during VSTM are sustained or rhythmic in nature. In the last empirical chapter to this thesis, I tested if response conflict depends on feature-specific sensory processing, or rather reflects the product of a domain general mechanism that is not specific to the source of interference. All chapters were characterized by an individual differences approach, in order to assess the functional role of different neural mechanisms associated with selective attention for goal-directed behavior. In chapter 6, I will discuss how the findings from the different studies in this thesis provide novel insights into the way our brain helps to overcome different forms of distraction that may otherwise impede accurate memory performance or the completion of planned actions that support goal-directed behavior in everyday life.

CHAPTER 2

Proactive, but not reactive, distractor filtering relies on local modulation of alpha oscillatory activity

Filter mechanisms that prevent irrelevant information from consuming the limited storage capacity of visual short-term memory are critical for goal-directed behavior. Alpha oscillatory activity has been related to proactive filtering of anticipated distraction. Yet, distraction in everyday life is not always anticipated, necessitating rapid, reactive filtering mechanisms. Currently, the oscillatory mechanisms underlying reactive distractor filtering remain unclear. In the current EEG study, we investigated whether reactive filtering of distractors also relies on alpha-band oscillatory mechanisms and explored possible contributions by oscillations in other frequency bands. To this end, subjects performed a lateralized change-detection task in which a varying and unpredicted number of distractors was presented both in the relevant hemifield, among targets, and in the irrelevant hemifield. Results showed that while proactive distractor filtering was accompanied by lateralization of alpha band activity over posterior scalp regions, reactive distractor filtering was not associated with modulations of oscillatory power in any frequency band. Yet, behavioral and post-hoc ERP analyses clearly showed that participants selectively encoded relevant information. Based on these results we conclude that reactive distractor filtering may not be realized through local modulation of alpha-band oscillatory activity.

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Introduction

Visual short-term memory (VSTM) - or the ability to temporarily keep information in mind - is fundamental for goal-directed behavior, but is limited in capacity to simultaneous maintenance of only 3 to 4 objects (Cowan, 2001). Efficient use of VSTM storage capacity thus necessitates selective encoding of goal-relevant information, preventing irrelevant or distracting items from consuming capacity. A large body of research shows that individual VSTM capacity is indeed strongly related to one's ability to filter out goal-irrelevant, distracting information (Fukuda & Vogel, 2009; McNab & Klingberg, 2008; Vogel, McCollough, & Machizawa, 2005). Distractor filtering thus seems to serve as a functional bottleneck in VSTM, selectively routing goal-relevant information into VSTM (Awh & Vogel, 2008), thereby ensuring that its capacity is effectively used.

Although the idea that distractor filtering serves an important role in VSTM is widely accepted, the functional networks of brain regions that enable efficient distractor filtering are not yet precisely delineated (Gazzaley & Nobre, 2012). A limiting factor here is that in the existing literature on the neural correlates of distractor filtering, the distinction between proactive vs. reactive mechanisms of distractor filtering is largely ignored in the interpretation of results (Geng, 2014). Yet, these two types of interference control may recruit distinct mechanisms: whereas proactive filtering or suppression entails prevention from interference (Bonnefond & Jensen, 2012), reactive interference control involves quick disengagement from irrelevant stimuli (Fukuda & Vogel, 2011). Everyday life situations usually demand a mixture of proactive and reactive distractor filtering (Peelen & Kastner, 2014): whereas particular behavioral goals allow intended, proactive routing of neural processing according to these goals, of course unexpected, but goal-irrelevant events, may also occur. At present, it remains unclear to what extent these two types of distractor filtering rely on distinct neural mechanisms.

Many studies have related proactive distractor filtering to a local enhancement of alpha band (8-12 Hz) oscillatory activity over regions processing task-irrelevant information, prior to stimulus presentation (cf., Kelly, Lalor, Reilly, & Foxe, 2006; Klimesch, Sauseng, & Hanslmayr, 2007; Mathewson et al., 2011; Mazaheri et al., 2014; Payne, Guillory, & Sekuler, 2013; Snyder & Foxe, 2010; Thut, Nietzel, Brandt, & Pascual-Leone, 2006). This increase in pre-stimulus alpha power is generally interpreted in terms of proactive inhibition of irrelevant sensory processing (Klimesch et al., 2007; Mazaheri & Jensen, 2010), allowing incoming perceptual information to be selectively routed to task-relevant brain regions and networks. This notion is supported by many reports of increased pre-stimulus alpha power over sensory cortices that represent distracting sensory input (Bonnefond & Jensen, 2012; Foxe & Snyder, 2011; Händel, Haarmeier, & Jensen, 2011). Yet, some studies have observed enhanced alpha activity over irrelevant posterior regions even in conditions where no distracting information was present, indicating that local modulations of alpha power in task-irrelevant brain regions are not necessarily linked to proactive distractor suppression (Myers, Walther, Wallis, Stokes, & Nobre, 2015; Noonan et al., 2016; Rihs, Michel, & Thut, 2007). In other words, although proactive inhibition has been associated with enhanced alpha power over task-irrelevant sensory regions, it is unclear if this modulation reflects distractor inhibition per se, or rather a more general attentional orienting towards task-relevant information.

Interestingly, findings from one EEG study suggest that alpha-band oscillatory activity may also play a role in reactive distractor filtering during VSTM retention (Sauseng et al., 2009). Specifically, this study found that during VSTM retention, alpha power scaled with the number of distractors (which could not be anticipated in advance) presented in the irrelevant visual hemifield, which was indicated by a cue preceding each stimulus display. These results suggest that alpha oscillations may not only serve as a proactive filter prior to encoding, but can be flexibly modulated to filter out unanticipated distractors reactively. Yet, to the best of our knowledge, these results have never been replicated. Moreover, although subjects did not know the exact number of distractors beforehand, distractor presence could be anticipated, as distractors were always present in the irrelevant hemifield in each trial (i.e., never in the same hemifield as the targets). This renders it unclear to what extent alpha oscillations play a role in reactive inhibition of distractors during VSTM retention in situations in which distractors may appear unexpectedly and/or in the attended hemifield.

Other studies that have so far examined the neural mechanisms involved in reactive distractor filtering, required when distractors are unpredicted, have mostly used event-related potentials (ERP) and functional magnetic resonance imaging (fMRI). This body of work suggests an important role for frontal brain regions and the basal ganglia in reactive distractor filtering. For example, a recent ERP study on distractor filtering and VSTM revealed a frontal distractor-sensitive signal during early stages of VSTM retention (Liesefeld, Liesefeld, & Zimmer, 2014). Interestingly, the amplitude of this signal was negatively related to later retention of irrelevant information, as reflected by the posterior contralateral delay activity (CDA; Vogel & Machizawa, 2004), in line with behavioral findings that suggest a close relationship between distractor filter ability and VSTM capacity. This pattern of findings also coarsely parallels earlier findings from fMRI studies, which indicate a critical role for frontal areas as well as the basal ganglia in protecting VSTM against irrelevant information, and for more occipital and parietal regions in actual storage of the information (Baier et al., 2010; Jha, Fabian, & Aguirre, 2004; McNab & Klingberg, 2008). Yet, the precise oscillatory mechanisms involved in reactive distractor filtering, specifically the role of alpha oscillations herein, remain to be elucidated.

The aim of the current EEG study was to enhance our understanding of oscillatory mechanisms involved in proactive and reactive distractor filtering, in relation to VSTM. To this end, we used a typical lateralized change detection task that allowed for proactive distractor filtering based on an attentional cue which indicated which hemifield would contain relevant, to-be-remembered stimuli (cf., e.g., Vogel & Machizawa, 2004). In order to examine the neural mechanisms underlying reactive filtering of unanticipated distractor load across hemifields, we varied the amount of distractors present in the relevant and irrelevant hemifield. Our main prediction was that alpha oscillatory activity, given its role in active inhibition, is involved in both proactive and reactive distractor filtering. First, we predicted to replicate previous studies showing greater alpha oscillatory activity over irrelevant versus relevant posterior scalp regions in anticipation of distraction (e.g. Händel et al., 2011). Secondly, we expected to replicate the previously reported load-dependent modulation of local alpha power over task-irrelevant scalp sites during suppression of distractors in the irrelevant hemifield (Sauseng et al., 2009). Our third and final prediction was that reactive suppression of distraction in the cued hemifield similarly relies on modulations of occipital alpha power. To this end, importantly, we used the spatially coarse lateralization response of alpha activity (contra- versus ipsilateral posterior alpha power) to infer distractor-related alpha enhancement and target-related alpha suppression within one hemifield. By itself, these processes would be hard to disentangle, given the close spatial proximity of target and distractors within the cued hemifield (see Fig. 1AB) and the poor spatial resolution of EEG. However, we applied the logic that if measured lateral posterior alpha power contralateral to the cued visual hemifield reflects a summation of these two signals, then the resulting lateralized alpha response should be reduced in the presence of distractors in the cued hemifield, compared to a situation in which the cued visual hemifield contains targets only. Hereby, we aimed to shed further light on the neurophysiological basis of different types of distractor filtering that aid selective retention of goal-relevant information in VSTM, in particular alpha oscillatory activity.

Methods

Participants

Participants took part in the experiment in exchange for course credits or monetary compensation. Participants had normal or corrected-to-normal vision, were neuropsychologically healthy, and were not colorblind. We obtained written and informed consent from each participant before the start of the experiment. The Ethics Committee of the Psychology faculty at the University of Amsterdam approved the experiment.

In total, 44 participants were tested. One participant was excluded due to technical problems during data recording, and two participants were excluded because more than half of the in the experiment were contaminated by muscle artifacts and/or horizontal eye movements. Ten additional participants were excluded because there was still residual eye movement related activity in the HEOG data after preprocessing (see section ‘EEG preprocessing’ for details). Analyses are based on the remaining 31 participants (mean age 22.4 years; SD 2.01 years; 22 F; 9 M).

Experimental task

We used a lateralized change-detection task with distractors (cf., e.g., Vogel et al., 2005). Participants were instructed to memorize the color of the targets (defined as squares) in the cued visual hemifield, and were explicitly told that the distractors (defined as circles) would not be relevant at any point throughout the experiment. Participants were asked to focus their eyes on fixation throughout a trial, and blink as little as possible in order prevent contamination of the EEG with blink-related artifacts. To be able to measure VSTM capacity, we manipulated the number of target stimuli (2 vs. 4 vs. 6). We also parametrically manipulated the number of distractors in the irrelevant visual hemifield (2 vs. 4) for different target loads (2 vs. 4) in separate conditions in order to investigate load-dependence of distractor suppression. Thus, as in Sauseng et al. (2009), although participants could anticipate distractors in the irrelevant field, they had no knowledge about the number of distractors in these trials. Lastly, we parametrically manipulated the number of distractors (0 vs. 2 vs. 4; circles) in the cued visual hemifield in order to investigate reactive distractor filtering in the relevant hemifield under different memory loads (2 vs. 4 targets; squares). When manipulating the number of distractors in the cued visual hemifield, we kept the number of stimuli in the irrelevant hemifield identical to the number of stimuli in the cued visual hemifield. In total, our experiment contained 9 conditions consisting of 100 trials each (see Figure 1B for an overview of the conditions with the numbers and types of stimuli). The task consisted of 25 blocks of 36 trials. Blocks were interspersed by self-paced breaks. Trials from the nine different conditions were administered in random order within each block.

Each trial started with a 200 ms presentation of an arrow shaped cue at fixation that indicated the to-be-attended hemifield on that trial (0.5 degrees of visual angle (dva); 50% left cue), followed by a 500 ms blank screen containing a central fixation-cross (0.5 dva). Note that this interval allowed subjects an additional 500 ms to orient their attention to the cued hemifield compared to the study by Sauseng et al. (2009), in which the memory display immediately followed the attention cue. Subsequently, the memory display was presented for 250 ms. This display was followed by a 1000 ms retention interval during which the fixation cross remained on the screen (see Figure 1A for a graphical display of the trial order). Next, a probe display was presented that was either identical to the memory display (50% of the trials, counterbalanced across cue sides), or was different because one of the target stimuli had changed color. Distractor stimuli could never change color. Participants needed to respond to the probe stimulus within 2000 ms. Sixteen participants responded using the keyboard (press Z key with the left index finger for no-change; press M key with the right index finger for change). Fifteen participants responded by pressing one of two response boxes placed on each arm rest (with the left index finger for no-change; with the right index finger for change). The fixation-cross remained visible throughout the entire trial to aid participants to maintain fixation. Trials were separated by variable inter-trial intervals, with a duration that was randomly jittered around 2000 ms (range: 1700-2300 ms).

The stimulus display consisted of a bilateral display with colored stimuli on a grey background (see Figure 1A). We positioned all stimuli within two square regions located left and right of fixation in the lower visual field (4.25 by 4.25 dva; positioned at 2 dva from the vertical meridian). Stimuli were presented in the lower visual field to obtain a relatively focal projection of stimulus-related oscillatory activity on the scalp (cf., Bahramisharif, Van Gerven, Heskes, & Jensen, 2010), such that changes in occipital activity related to stimulus processing in one hemifield should be reflected in the aggregate of activity measured at these focal contralateral scalp sites. Target stimuli were colored squares (.75 dva); distractor stimuli were colored circles (.85 dva). Colors of stimuli were randomly selected from eleven highly distinguishable colors on each trial. A color would never appear twice in one visual hemifield, and new target colors on change trials were always different from the colors of the stimuli presented in the cued visual field. Stimulus positions were constrained such that individual stimuli would never touch or overlap.

Procedure

Participants were seated at a 90 cm distance from the screen. Before the start of the experiment, participants practiced two blocks of the task of 20 trials each (low load conditions only) to become familiar with the task and the response buttons. Participants were given extensive task instructions before the start of the practice task. During the first practice block, participants received immediate feedback on their response (correct/incorrect/late). In the second practice block immediate feedback was no longer provided, in order to prepare subjects for the experimental phase, in which subjects also did not receive feedback on their performance.

Behavioral data analysis

Behavioral analyses were based on trials in which participants responded in time (within 2000 ms), excluding trials containing fast, uninformed responses (reflected by reaction times < 200 ms). Using participants' HEOG data, we discarded trials in which participants made an eye movement away from fixation (for details on eye movement detection, see the section below). All trials in which participants responded in time and maintained fixation were used for behavioral data analysis. This procedure yielded an average of 837 trials (93% of the total number of trials) per participant (SD 58, range: 701-893).

The effects of memory load and distractor load in the cued and irrelevant visual hemifield on accuracy of performance were tested using repeated measures ANOVAs. The corrected degrees of freedom (Greenhouse-Geisser correction) are reported when the assumption of sphericity was violated (tested using Mauchly's test of sphericity). VSTM capacity was computed using Pashler's index of VSTM capacity (K_p; Pashler, 1988), as the probe in our change detection task required whole-display recognition (Rouder, Morey, Morey, & Cowan, 2011). Correlations between VSTM capacity and the effect of distractors on performance were assessed using a Pearson correlation coefficient. Based on previous research (Fukuda & Vogel, 2009; Vogel et al., 2005) we a priori predicted an inverse relationship between the effect of distractors on performance and VSTM capacity, and used a one-tailed test to assess the significance of the correlation ($\alpha = .05$).

EEG data collection and preprocessing

EEG data were recorded at 512 Hz from 64 channels placed according to the international 10–20 system using a Biosemi set-up. External electrodes were used to measure horizontal and vertical eye movements, and were placed next to the right and left eye (HEOG), and below and above the left eye (VEOG). Reference electrodes were placed on the earlobes.

Offline, EEG data were rereferenced to the average-earlobes. Data were high-pass filtered at 0.05 Hz and were epoched from –2.2 to +3.3 s surrounding stimulus onset (to avoid edge artifacts resulting from wavelet filtering in the time-frequency analysis) and baseline-corrected by removing the average activity in the 200 ms time window preceding presentation of the cue for each channel and trial. The epoched data was visually inspected and trials containing EMG activity or other artifacts on multiple electrodes that were not related to blinks, were manually removed. We applied single-trial interpolations of electrodes that displayed artifactual activity at the single-trial level, for which interpolation of the channel for the entire experiment would have been too stringent. Electrodes that contained noisy data throughout the majority of the experiment were temporarily set to zero to be interpolated after ICA decomposition (interpolation was postponed in order to avoid reducing the rank of the data before running independent component analysis (see van Driel, Knapen, van Es, & Cohen, 2014). Independent components analysis was computed on the cleaned dataset using EEGlab software (Delorme & Makeig, 2004). Components containing blinks or other artifacts that could be clearly distinguished from brain-driven EEG signals were subtracted from the data. As in the behavioral analyses, error trials and trials in which participants responded too early (< 200 ms) or too late (> 2000 ms), were excluded from the analysis. Based on manual inspection of the HEOG trace, trials containing horizontal eye movements were removed from further analysis. Only participants who displayed no residual HEOG activity after preprocessing were included in subsequent analyses. To determine if residual HEOG activity was present, we subtracted the average HEOG activity on left-cue trials from that on right-cue trials, and examined the extent to which the trial-average difference deviated from zero. Participants for whom the trial average difference between left and right cue trials showed an absolute difference of more than 3 mV for a consecutive period of 50 ms or more were excluded from the analyses (cf. Luck, 2014). Eleven participants were excluded this way. In the remaining group of participants, an average of 642 (SD 76.8, range: 516-781) artifact-free trials (71% of total number of trials) per participant were included in further analyses. Next, the EEG data were transformed such that on all trials, the left hemisphere was contralateral to stimulus presentation. Hereto, we swopped data at symmetrical electrodes (e.g., F1 and F2) along the midline (Iz to FPz) in trials with a leftward cue, so that data in all trials reflected activity following a rightward attentional cue. After this transformation, the data were collapsed across cue directions (left vs. right).

Time-frequency analysis of the EEG-data

We subtracted the evoked activity from the EEG-data before time-frequency analysis (cf. Sauseng et al., 2009). Subsequently, we applied a surface Laplacian on the data in order to increase topographical specificity and reduce the effects of volume conduction (Cohen, 2014; Srinivasan, Winter, Ding, & Nunez, 2007). We used a filter with a 10th order Legendre polynomial and a smoothing parameter (λ) of 10^{-5}. The units of the data after this transform are $\mu V/cm^2$.

Frequency band-specific power was extracted using time-frequency decomposition of the EEG data for each channel and condition with in-house written Matlab routines. Single-trial stimulus-locked data were convolved with a family of complex Morlet wavelets, defined as Gaussian-windowed complex sine waves:

$$e^{i2\pi ft}\, e^{-t^2/2s^2}$$

Here, *i* reflects the complex operator, *t* reflects time, and *f* reflects frequency. Frequencies increased from 1 to 40 Hz in 20 logarithmically spaced steps. The width of the wavelet for each frequency (σ) was set as $n/2\pi f$, where *n* is the number of wavelet cycles, scaled logarithmically from 3 to 10. Power (p) was extracted from the signal as the squared magnitude of the complex signal ($Z(t)$) resulting from the convolution ($p(t) = \text{real}[z(t)]^2 + \text{imag}[z(t)]^2$). After time-frequency decomposition, power was converted to a decibel-scale (dB), which enables comparison of amplitude across frequency bands (dB power = 10*log10 [power/baseline]), using a baseline time window between 500 and 200 ms preceding presentation of the cue. The data were downsampled to 40 Hz for computational purposes after wavelet convolution.

Electrode selection and statistical analysis of time-frequency data

To examine the oscillatory mechanisms underlying reactive filtering of distracting information, we tested whether lateralized occipital alpha power was sensitive to distractor load in the cued and/or irrelevant hemifield. To this end, we averaged the power of alpha (8-12 Hz) activity during the delay interval (350 – 1250 ms post- stimulus) at occipital electrodes (PO3, PO7, O1 vs. PO4, PO8, O2 for contralateral vs. ipsilateral sites) across conditions. In order to study the potential time-frequency equivalent of the ‘frontal bias signal’ located at frontal sites (Liesefeld et al., 2014), we selected time-frequency windows based on the peaks in the condition-average activity at frontal channels (see Figure 3). These condition-averages were then subjected to repeated measures ANOVA’s with the factors i) distractor load (2 vs. 4 in the irrelevant hemifield, cf., Sauseng et al., (2009), or 0 vs. 2 vs. 4 in the relevant hemifield), ii) memory load (2 vs. 4), and iii) hemisphere (contralateral vs. ipsilateral). For all statistical tests we report the corrected degrees of freedom (Greenhouse-Geisser correction) when the assumption of equal variances was violated (tested using Mauchly's test of sphericity). Correlations between behavioral variables of interest, such as VSTM capacity (K_p) and time-frequency power were tested using Spearman rank correlations, since power-data is often not normally distributed (Cohen, 2014).

ERP analyses

We also aimed to replicate previously reported effects of distractors presented among targets in the relevant hemifield on ERP components related to distractor storage (the CDA) and distractor signaling (the frontal bias signal; Liesefeld et al., 2014; Vogel et al., 2005). ERP analyses were performed using EEGLAB (Delorme and Makeig, 2004) and Matlab (The MathWorks), using in-house written code to extract the CDA and the frontal bias signal. For computation of the CDA, data were first baselined using a 200 ms time window preceding stimulus presentation (Spronk, Vogel, & Jonkman, 2012) and low-pass filtered using an 80 Hz low-pass filter (Hamming window sinced FIR filter, using the function pop_eegfiltnew). The CDA was computed as the difference between the average activity at posterior channels in the hemisphere contralateral (P3, P5, P7, P9, PO3, PO7, O1) and ipsilateral (P4, P6, P8, P10, PO4, PO8, O2) to target presentation, in the time window between 350 to 1250 ms after stimulus onset. An additional cleaning procedure was applied to the resulting difference wave to remove slow drifts resulting from our low cut-off frequency (.05 Hz) of our high-pass filter from our ERP of interest, which gained strong influence on the trial averages, due to the long time windows used to compute the CDA. To minimize their influence, the data were trimmed by first sorting trials according to amplitude and subsequently removing the 10% most extreme values at each tail of the distribution for each condition (cf., Rousselet & Pernet, 2011; Wilcox, 2012). This way, the original central tendency of the condition-specific CDA waveforms was maintained, but trials in which the CDA obtained an extreme value due to drifting that may obscure condition differences were selectively removed.

We also focused our ERP analyses on the frontal bias signal observed at frontal sites early during VSTM retention. Based on the latency and topography of this ERP reported by Liesefeld et al. (2014) and visual inspection of our condition-averaged data, we computed the frontal bias signal at a set of frontal electrodes (F1, F3, AF3, Fz, Afz, AF4, F4, F2) in a time window between 240 and 290 ms post-stimulus (Liesefeld et al., 2014).

We first examined if distractors could effectively be reactively prevented from entering VSTM storage. To this end, the effect of distractors on CDA amplitude was quantified by comparing the condition-average activity in the condition with memory load 2 with and without distractors, for different levels of distractors (2T vs. 2T2D; 2T vs. 2T4D). Then, we assessed if individuals with higher VSTM capacity were generally more successful from keeping distractors from entering VSTM by correlating the distractor-related amplitude of the CDA with VSTM capacity (K_p) using a Pearson correlation test. Next, we aimed to replicate the previously reported effect of general distractor-presence on the frontal bias signal, and averaged the ERP in the time window of interest using the conditions containing targets only (2T; 4T; 6T), and compared this to the average ERP in the conditions that also contained distractors in the cued visual hemifield (2T2D; 2T4D; 4T2D; 4T4D). Finally, we examined if individuals with a stronger frontal bias signal generally displayed a reduced influence of distractors on CDA amplitude, and correlated the distractor-related amplitudes of the CDA and the 'frontal bias signal' for 2 distractors and memory load 2 (2T2D vs. 2T) using a Pearson correlation test. Based on previous research (Liesefeld et al., 2014; Vogel et al., 2005) we had strong expectations of an inverse relationship between the effect of distractors on the CDA and VSTM capacity, as well as the distractor-related amplitude of the 'frontal bias signal', and used one-tailed tests ($\alpha = .05$) to assess the significance of the correlation coefficients. For plotting purposes, ERP waveforms were temporally smoothed (using a moving average method, with a 100 ms span). Statistical analyses were based on the non-smoothed datasets. In all figures displaying ERP waveforms, negative voltages are plotted upwards.

Results

Behavior

VSTM performance and capacity

Accuracy of performance decreased with memory load ($F_{2,60} = 304.58$, $p < .001$): planned contrasts showed that performance decreased when remembering 4 instead of 2 (82% vs. 96% correct; $F_{1,30} = 213.69$), as well as 6 instead of 4 items (71% vs. 82% correct; $F_{1,30} = 375.84$, $p < .001$; see Figure 1). In line with previous findings, the average value of K_p was 3.07, and ranged between 1.94 and 4.36 across participants, indicating an average VSTM storage capacity of about 3 objects and large inter-individual differences in storage capacity.

Effects of distractors on behavior

We first examined the extent to which distractors in the irrelevant hemifield impaired task performance (see Figure 1C). A repeated measures ANOVA with the factors distractor load in the irrelevant hemifield (2 vs. 4) and memory load (2 vs. 4) revealed no main effect of the factor distractor load ($F_{1,30}$ = .57, *p* = .457), but a significant interaction between distractor load and memory load ($F_{1,30}$ = 5.15, *p* = .031). This interaction was driven by small distractor-related performance effects of opposite sign across memory loads: a high distractor load in the irrelevant visual hemifield tended to impair performance under high memory loads (-1.7 %; t_{30} = 1.564, *p* = .128), but improve performance under low memory loads (+ .8 %; t_{30} = -1.954, *p* = .060). Thus, these individual post hoc contrasts as well as the main effect of distractor load were non-significant. This suggests that the effect of distractors in the irrelevant hemifield, which could be anticipated based on the attentional cue, on performance was very small or even negligible.

Next, we examined to what extent distractors presented among the targets in the relevant hemifield influenced performance, and if their effect depended on memory load. To this end, a repeated measures ANOVA was conducted with the factors distractor load in the cued hemifield (0 vs. 2 vs. 4) and memory load (2 vs. 4; note that

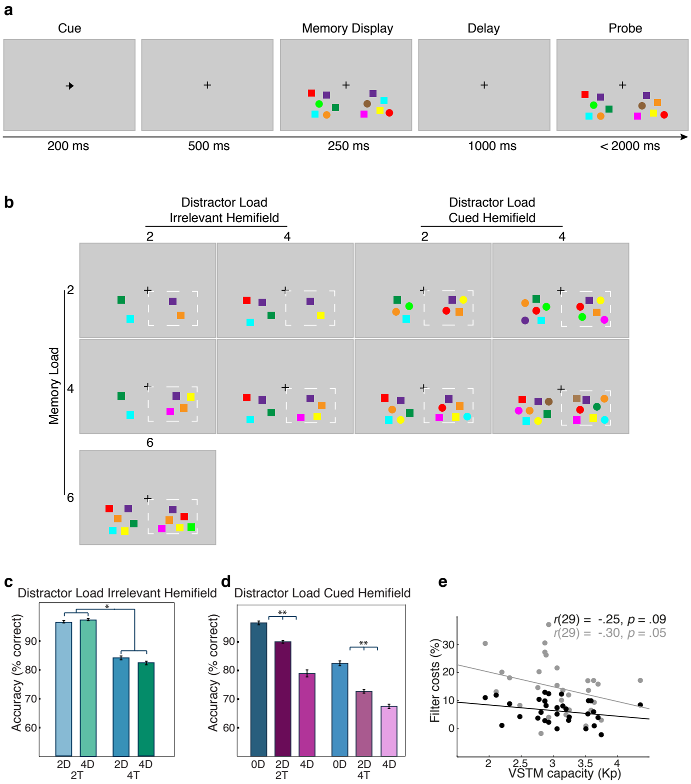

Figure 1. VSTM task design and performance. A) Example of a trial. In this example, subjects had to remember the color of 4 targets (squares) presented among 2 distractors (circles) in the cued visual hemifield. B) Overview of the nine experimental conditions. Dashed white rectangles (not visible in the actual experiment) indicate the attended hemifield (right cue trials). C) The effect of distractors in the irrelevant visual hemifield on accuracy of performance. As can be seen, distractors in the irrelevant visual hemifield did not affect performance. D) The effect of distractors in the cued visual hemifield on accuracy of performance. Distractors in the cued visual hemifield significantly impaired performance. This effect was dependent on memory load. E) The relationship between filter costs (effect of distractors on performance; % performance decline) and VSTM capacity for 2 (black dots) and 4 (grey dots) distractors in the cued hemifield. Error bars: ± 1 SEM.

this analysis was performed on the subsample of participants for whom all required levels of distractor load were included in the task; $n = 15$). Results revealed a main effect of the factor distractor load ($F_{1.4,19.3} = 58.24$, $p < .001$), as well as a main effect of memory load ($F_{1,14} = 282.30$, $p < .001$). Planned contrasts showed that performance decreased with increasing numbers of distractors (-8.2% for 0 vs. 2 distractors; $F_{1,14} = 50.27$, $p < .001$; -8.2 % for 2 vs. 4 distractors; $F_{1,14} = 61.52$, $p < .001$; see Figure 1D). We observed a trend towards an interaction between distractor load and memory load ($F_{1.5,20.8} = 3.04$, $p = .082$), where the performance decrease due to 2 instead of 0 distractors was bigger under high memory loads (- 10%) than low memory loads (-7%; $t_{14} = -2.12$, $p = .053$), whereas the decrease due to 4 instead of 2 distractors was biggest under low memory loads (-11% vs. -5%; $t_{14} = .96$; $p = .355$). This pattern of findings suggests that reactive filtering mechanisms of within-hemifield distractors are imperfect: the presence of distractors in the cued visual hemifield impaired memory performance.

Previous research has shown that the extent to which within-hemifield distractors impair performance (or filter efficiency) predicts individual VSTM capacity (e.g., Fukuda & Vogel, 2009). In line with this observation, the correlation between $K_{p\text{-}max}$ and the effect of distractors in the cued visual hemifield for memory load two reached trend-level significance for two distractors (2T0D vs. 2T2D; $r_{29} = -.25$, $p = .085$), but was significant for four distractors (2T0D vs. 2T4D; $r_{29} = -.30$, $p = .050$). Previous research used Cowan's K ($K_{c\text{-}max}$) to index VSTM capacity (e.g., Vogel & Machizawa, 2004). Although $K_{p\text{-}max}$ is considered a more proper index of VSTM capacity for change detection task requiring whole-display recognition (Rouder, Morey, Morey, & Cowan, 2011), we post-hoc analyzed the relationship between $K_{c\text{-}max}$ and the effect of distractors on performance in order to be able to directly compare our results to previous research on the relationship between VSTM capacity and distractor filtering. This revealed significant correlations between $K_{c\text{-}max}$ and filter costs for two as well as four distractors ($r_{29} = -.34$, $p = .030$; $r_{29} = -.36$, $p = .023$ respectively). Thus, replicating earlier findings we found that distractors generally influenced performance less in individuals with a higher VSTM capacity, but more robustly using $K_{c\text{-}max}$ than $K_{p\text{-}max}$.

Oscillatory dynamics of distractor filtering

The role of occipital alpha lateralization in distractor filtering

We first examined if we could replicate the previously reported cue-induced lateralization in pre-stimulus alpha-band oscillatory activity. As can be seen in Figure 2BC, alpha power lateralization developed well before memory display onset, after the presentation of the spatial cue. This effect reflected significantly stronger pre-stimulus alpha power activity over irrelevant vs. relevant posterior regions (300-100 ms preceding stimulus presentation; $t_{30} = 8.70$; $p < .001$), suggesting that subjects may have proactively suppressed processing of distracting information in the irrelevant hemifield. To

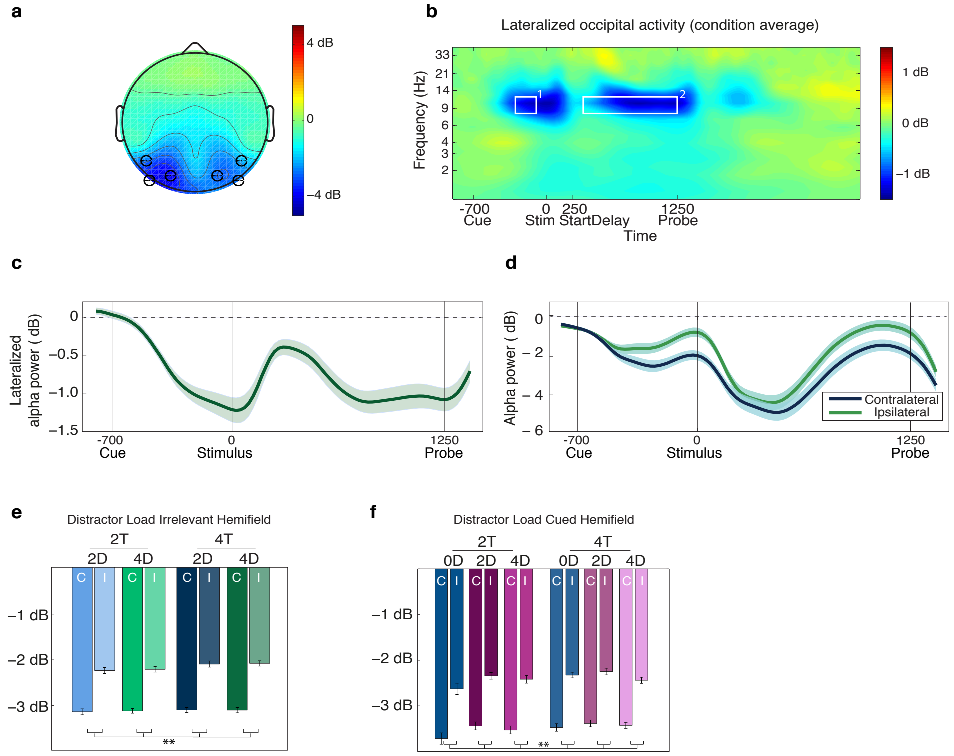

Figure 2. Lateralized alpha oscillatory activity is not reactively modulated by distractor load. A) Topographical distribution of condition-average alpha activity (8-12 Hz) during the retention interval (350-1250 ms). Black electrodes depict the electrodes used for statistical analysis of the effects of the attention (cue) direction and distractor load. Note that in this plot, the left hemisphere is the hemisphere contralateral to the cued hemifield, whereas the right hemisphere is ipsilateral to the cued hemifield. B) Time-frequency representation of condition-average lateralized activity throughout an entire trial at occipital electrodes contralateral (PO3, PO7, O1) vs. ipsilateral (PO4, PO8, O2) to the cued hemifield. The white rectangles reflect the time-frequency windows used for 1) the correlation between pre-stimulus lateralized alpha power and behavior, and 2) the effects of distractor load and memory load on alpha power during VSTM retention. C) Time-course of condition-average lateralization of alpha activity (8-12 Hz; contralateral minus ipsilateral electrodes). Alpha lateralization increased prior to presentation of the stimulus and probe. D) Time-course of condition-average occipital alpha activity (8-12 Hz) at relevant (contralateral; blue line) and irrelevant (ipsilateral; green line) electrodes. Alpha power followed a similar pattern across hemispheres, but with stronger suppression in the contralateral compared to the ipsilateral hemisphere. E) Bar plots showing the effect of distractor load in the irrelevant hemifield (2 vs. 4) under different memory loads (2 vs. 4) on alpha power in the hemisphere contralateral (C) and ipsilateral (I) to the cued hemifield. Alpha power was lower in the hemisphere contralateral to the cued hemifield regardless of the number of distractors in the irrelevant hemisphere. F) Bar plots showing the effect of distractor load in the cued hemifield (0 vs. 2 vs. 4) under different memory loads (2 vs. 4) on alpha power in the hemisphere contralateral (C) and ipsilateral (I) to the cued hemifield. Alpha power was lower in the hemisphere contralateral to the cued hemifield and not modulated by the number of distractors in the relevant hemifield. Error bars: ± 1 SEM.

explore this possibility further, we examined whether the degree of cue-related alpha lateralization (300-100 ms preceding stimulus presentation) predicted performance, by testing whether lateralization of prestimulus alpha power was predictive of the subsequent effect of distractors in the irrelevant hemifield on VSTM performance (cf., Händel et al., 2011). However, we found no evidence for a relationship between stronger lateralization and distractor load related performance decline under low memory loads (2T; $r_{29} = -.18$, $p = .342$) or high memory loads (4T; $r_{29} = .10$, $p = .609$; Spearman rank correlations). To examine the possibility that individual differences in VTSM capacity may have masked this relationship, we post-hoc repeated this analysis but now controlling for VSTM capacity ($K_{p\text{-}max}$). However, the relationship between lateralized pre-stimulus alpha power and the effect of distractors in the irrelevant field on performance across individuals remained non-significant when controlling for VTSM capacity ($r_{28} = -.118$, $p = .536$ for trials with memory load 2; $r_{28} = .047$, $p = .803$ for trials with memory load 4). The lack of such a relationship in combination with the lack of an effect of irrelevant-hemifield distractors on VSTM performance (reported in the previous section), may indicate that *all* subjects effectively filtered the distracting information in the irrelevant hemifield. Possibly, the longer time interval between the cue and the memory display allowed all participants to proactively establish alpha lateralization, and thereby gate these distractors from storage in VTSM.

Strikingly, lateralized alpha power was not affected by the number of distractors in the irrelevant hemifield during VSTM retention, in contrast to an earlier report by Sauseng et al. (2009). That is, a repeated measures ANOVA with the factors distractor load in the irrelevant visual field (2 vs. 4), memory load (2 vs. 4), and hemisphere (contralateral vs. ipsilateral to the cued hemifield) only revealed a main effect of hemisphere ($F_{1,30} = 55.89$, $p < .001$), with lower alpha power at contralateral (M = -3.14 dB) as compared to ipsilateral sites (M = -2.18 dB), regardless of the number of ipsilateral distractors. Thus, contrary to our second prediction, ipsilateral alpha power during VSTM retention was not sensitive to distractor load ($F_{1,30} = .05$, $p = .82$; see Figure 2E) when subjects were given sufficient time to orient attention before the memory display was presented.

Moreover, in contrast to our third prediction, lateralized occipital alpha power was also not reactively modulated by distractors in the cued visual hemifield during the retention interval (see Figure 2F; note that this analysis was again performed on the subsample of participants for whom all required levels of distractor load were included in the task; *n* = 15). There was no effect of distractors in the cued visual field (0 vs. 2 vs. 4) under different memory loads (2 vs. 4) on occipital alpha power across both hemispheres (contralateral vs. ipsilateral; $F_{2,28} = 2.36$, $p = .113$), and also no interaction between the effect of distractors and hemisphere ($F_{1.46,2.46} = .51$, $p = .605$). The only significant effect was a main effect of hemisphere ($F_{1,14} = 32.94$, $p < .001$), reflecting that alpha power was always lower over the hemisphere contralateral to the cued visual hemifield (M = -3.49 dB) than over the ipsilateral hemisphere (M = -2.40 dB). Furthermore, post-hoc analyses revealed no evidence for a relationship between the effect of distractors in the cued hemifield on lateralized occipital alpha power during the delay period and their effect on accuracy of performance (comparing 2 vs. 0 and 4 vs. 0 distractors), or VSTM capacity (all *p's* > .07), indicating that the effect of distractors on lateral occipital alpha power did not vary as a function of performance. Thus, our findings do not provide evidence for a role for lateralized alpha oscillatory activity in reactive distractor filtering during VSTM retention.

Exploratory analyses: oscillatory mechanisms involved in reactive, within-hemifield distractor filtering

Reactive distractor filtering may also rely on non-lateralized neural mechanisms in frequency bands other than alpha. Therefore, we next explored the involvement of other low-frequency oscillatory mechanisms in reactive distractor filtering. Here we focused on effects in the theta (3-7 Hz) and beta (14-22 Hz) frequency ranges in the entire retention interval, as we had no specific predictions on the frequency characteristics and timing of the effect. Relevant time-frequency windows to subject to statistical testing were based on visual inspection of the condition average data. Note that this procedure is essentially orthogonal to the contrast of interest, and therefore does not lead to biased results of later statistical tests. Topographical representations of the data revealed a positive theta and beta peak at AFz and Fz with a latency and topography resembling that of the frontal bias signal ERP reported by Liesefeld et al. (2014) (see Figure 3A and 3B). Therefore, these electrodes were selected to explore a relationship between oscillatory activity in these frequency bands and reactive distractor filtering. Figure 3C shows the time-frequency representation of condition-average oscillatory power throughout the trial. Based on the peaks in the condition-averaged activity at AFz and Fz, we selected low theta activity (2-5 Hz) between 350 and 950 ms post-stimulus, and low beta activity (12-18 Hz) between 550 and 1150 ms post-stimulus, for statistical testing of the effect of distractors in the cued visual hemifield on these different frequency bands (see the black boxes in Figure 3C).

A repeated measures ANOVA on the average theta activity in this time window with the factor distractors in the cued hemifield (0 vs. 2 vs. 4), for trials with memory load 2 did not reveal an effect of distractor load on theta power during this time window ($F_{1,30} = .36$, $p = .698$; see Figure 3D-F). Frontal beta activity was also not modulated by distractor presence ($F_{1,30} = .45$, $p = .639$). Thus, these exploratory analyses did not

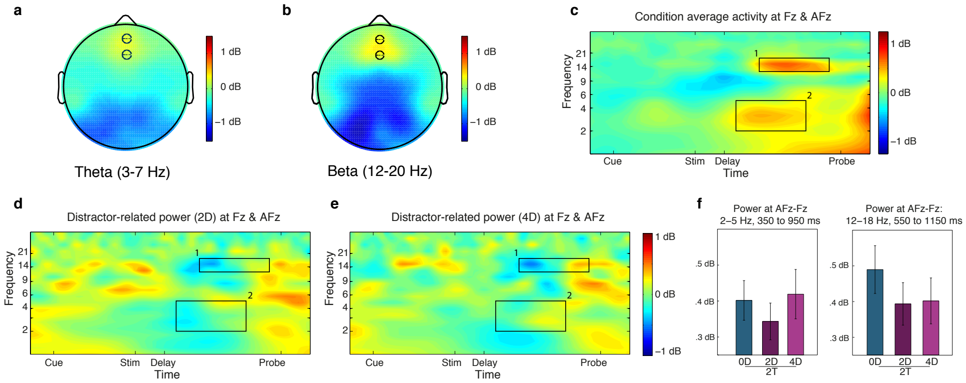

Figure 3. Effects of distractors on frontal theta and beta activity. A) Topographical distribution of condition-average theta activity (3-7 Hz) during the retention interval (350-1250 ms). B) Topographical distribution of condition average low beta activity (12-20 Hz) during the retention interval (350-1250 ms). C) Full time-frequency spectrum of the condition average power at electrodes AFz and Fz. Black rectangles reflect the time-frequency windows that were used for statistical analysis of the effects of distractors in the cued hemifield on theta and beta oscillatory power. D) Time-frequency representation of the effect of 2 distractors in the cued hemifield, for trials with memory load 2 (2T2D vs. 2T0D). E) Time-frequency representation of the effect of 4 distractors in the cued hemifield, for trials with memory load 2 (2T4D vs. 2T0D). F) Bars depict the power across conditions with 0, 2 or 4 distractors, for the time-frequency windows in theta (left panel; 3-7 Hz, 350-950 ms) and beta (right panel; 12-18 Hz, 550-1150 ms) used for statistical testing. Distractor load did not modulate theta or beta power in the selected time windows. Error bars: ± 1 SEM.

provide evidence for the existence of a non-lateralized oscillatory correlate of reactive distractor filtering in service of VSTM.

Exploratory analyses: single-trial regression to elucidate oscillatory mechanisms involved in distractor filtering

Given the above null findings, which may be somewhat surprising in light of the well-known role of alpha oscillations in inhibition of sensory processing, finally, we performed single-trial multiple regression on our EEG data. This allowed us to examine possible effects of the factors of interest in a more data-driven manner, to make sure that we did not miss any distractor-related power modulations by restricting our statistical analyses to selected electrodes and time-frequency windows. Single-trial analysis was performed using robust regression (using iteratively reweighted least squares; cf., Cohen & Cavanagh, 2011; Wager, Keller, Lacey, & Jonides, 2005). We used the design matrix of our task as predictors, with the factors cue side, memory load, distractor load in the cued hemifield, and distractor load in the irrelevant hemifield. Additionally, we included possible interactions between the effects of cue side and memory load, distractor load in the cued visual field, and distractor load in the irrelevant field as predictors. The regression was performed using the following equation: Y = INT + b_1CUE + b_2ML + b_3DLC + b_4DLI + b_5CUE.ML + b_6CUE.DLC + b_7CUE.DLI + E. Here, Y is the data vector with oscillatory power across trials. INT is the intercept (accounting for the Power Law scaling of frequencies; Cohen & Cavanagh, 2011) and E is unexplained variance. CUE is a vector that codes the side of the attentional cue (left or right). ML is a vector representing the memory load in the cued hemifield, DLC is a vector representing the distractor load in the cued hemifield, and DLI is a vector representing the distractor load in the irrelevant hemifield. The last three predictors represent interaction terms between cue side and the factors memory load, and distractor load in the cued (DLC) and irrelevant hemifield (DLI).

We included single-trial time-frequency representations of the data covering the time between presentation of the attentional cue and the probe (-700 to 1250 ms), 20 frequencies ranging from 1 to 40 Hz (see Methods section for details), and all channels, to compute the beta weights for each predictor for each subject separately. The single-trial power data were normalized (mean-centered and scaled by their standard deviation) before performing the regression. Note that we did not flip any of the trials based on cue-direction in this analysis, in order to be able to estimate the regression weights for the effect of cue side. The result of the regression was a subject by channel by time by frequency matrix with beta values for each predictor in our model. In order to be able to compare the estimated beta weights across subjects, we normalized the beta values by their standard error (Cohen & Cavanagh, 2011). Statistical significance of the beta weights was assessed at the group-level, and was done by testing the beta weights against zero for each channel*time*frequency point ($\alpha = .01$). Subsequently, the significant channel*time*frequency points were cluster-corrected by removing data points that were not included in a cluster exceeding the size of the 99th percentile of maximum cluster sizes observed under the null-hypothesis. The distribution of cluster-sizes under the null-hypothesis was estimated using 1000 permutations of the data on which we randomly changed the sign of the beta weights across participants, clustered the channel*time*frequency points with significant beta weights, and extracted the maximum cluster size across the remaining clusters. Cluster-level statistics were computed separately for each predictor included in the model.

We used the predictor cue side to assess whether the regression could reproduce the results from the trial-average data showing lateral occipital alpha power being responsive to the direction of the attentional cue. Figure 4 depicts the topographical and time-frequency characteristics of the group-averaged standardized regression coefficients for the predictor cue side. Black outlines represent clusters of data points significantly affected by the predictor of interest. Robust regression of the factor cue that allowed proactive preparation for distractors in the irrelevant hemifield, revealed four significant clusters in which bilateral alpha band activity was affected by the direction of the cue. Two of these clusters developed following presentation of the spatial cue prior to stimulus presentation (see Figure 4A), whereas the other two clusters developed during VSTM retention (Figure 4B), prior to presentation of the probe. Critically, these results from our data-driven approach closely mirror the findings of lateralized alpha

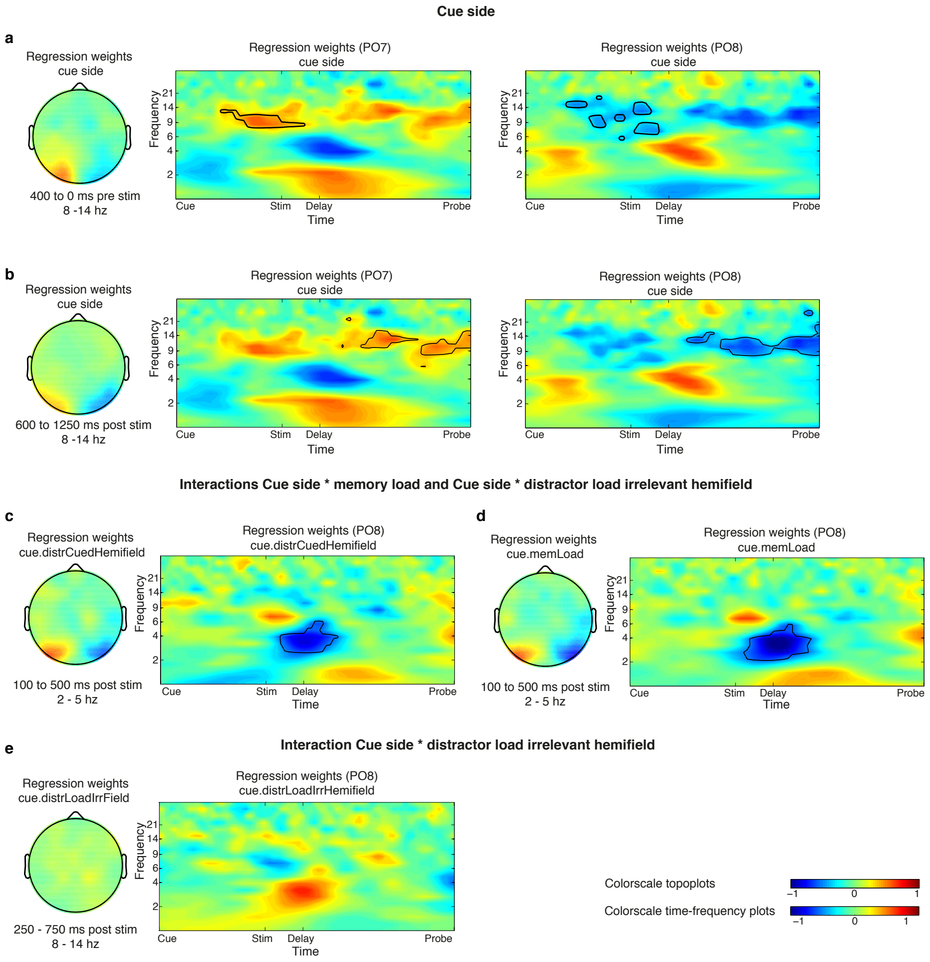

Figure 4. Results from the data-driven single-trial regression analysis. Topoplots and time-frequency representations display the group-average standardized beta weights for the predictors included in the single-trial regression. Clusters of activity significantly affected by factors of interest are depicted by black outlines. The data-driven analysis revealed greater alpha activity over ipsilateral vs. contralateral scalp regions before stimulus (A) and probe (B) presentation. Moreover, both distractor load and target load in the relevant hemifield modulated early theta activity, as indicated by significant interactions between cue side and distractor load in the cued hemifield (C), and between cue side and memory load (D), respectively. E) Distractor load in the irrelevant hemifield was not associated with modulations of lateralized (alpha) oscillatory activity, as the interaction between cue side and the number of distractors in the irrelevant hemifield did not reach significance in any time-frequency window across electrodes.

power as a mechanism involved in general attentional orienting depicted in Figure 2BC.

Interestingly, our data-driven approach also revealed an early interaction between cue direction and distractor load in the cued hemifield (Figure 4C). Specifically, between ± 100-500 ms post-stimulus presentation, contralateral theta band (2-5 Hz) activity increased as a function of number of distractors in the relevant hemifield (please note that the topography of this effect differs from the topography of the theta band activity displayed in Figure 3F; see Figure 3A). While one could interpret this as an effect of distractor load, contralateral theta band activity over similar scalp regions also increased in this same time window as a function of the number of targets presented, as indicated by an interaction between cue direction and memory load (Figure 4D). These observations together indicate that early contralateral theta activity may have increased as a function of the number of visual stimuli presented in the relevant hemifield, regardless of whether they were targets or distractors. In line with this conclusion, the beta weights of the two clusters were strongly correlated across participants ($r_{29} = .866$, $p < .0001$). No other clusters displaying an interaction between cue direction and distractor load in the relevant hemifield were observed. It is possible that individual differences in VSTM capacity masked effects of distractors at the group level. To address this possibility, we post hoc computed the significance of the regression weights for low and high VSTM capacity subjects separately (subgroups defined using a median split of $K_{p\text{-}max}$). However, there were no clusters for which the interaction between cue side and number of distractors in the cued hemifield reached significance in either VSTM subgroup. Thus, our more data-driven approach also did not reveal an oscillatory mechanism selectively involved in reactive suppression of distraction in the relevant hemifield.

Similarly, no significant interaction was observed between the number of distractors in the irrelevant visual field and the cued hemifield during VSTM retention. This indicates that the above reported non-replication of a role for lateralized occipital alpha activity in reactive filtering of distractors in the irrelevant hemifield (as reported by Sauseng et al., 2009) cannot just be attributed to our choice of the electrodes and time-frequency window used in that analysis. Inspection of the uncorrected beta weights (Figure 4E) also did not reveal any evidence for the involvement of ipsilateral occipital alpha activity in distractor filtering of distractors in the irrelevant visual hemifield. Thus, although we observed a clear effect of spatial attention on lateralized occipital alpha activity, we found no evidence for reactive modulation of lateralized alpha activity during VTSM in the presence of distractors using a data-driven approach either.

We also inspected the results of the regression for main effects of distractor load in the cued and irrelevant field to identify oscillatory mechanisms that may underlie

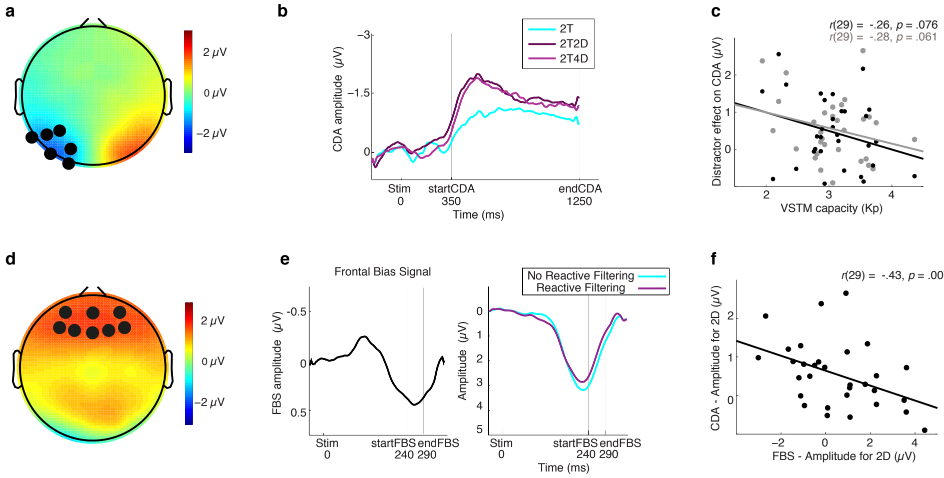

Figure 5. ERP components captured (failed) reactive distractor filtering. A) Scalp topography of the condition-average CDA (contralateral minus ipsilateral activity) in the time window 350-1250 ms post presentation of the memory array. Black dots represent the electrodes used to compute the CDA. Contralateral electrodes are depicted over the left hemisphere. B) CDA waveforms for the memory load 2 conditions with 0, 2 and 4 distractors. C) Correlation between individual VSTM capacity (Kp) and the efficiency of distractor filtering (excluding distractors from VSTM storage) as indicated by the effect of 2 (black data points) and 4 (grey data points) distractors on the amplitude of the CDA. D) Scalp topography of the condition-average frontal bias signal between 240-290 ms post-stimulus. Black dots represent the electrodes used to compute the frontal bias signal. E) FBS waveform during the first 300 ms following stimulus presentation (left panel), and ERP waveforms in the same time window for the conditions without distractors (no reactive filtering) and with distractors (reactive filtering) that were used to compute the FBS (right panel). F) Distractor signaling, as reflected by the distractor-related amplitude of the frontal bias signal, was negatively related to unnecessary storage of distractors in VSTM, as indicated by the increase in CDA amplitude when 2 versus no distractors were present at memory load 2 (2T2D vs. 2T0D), across participants.

distractor detection or suppression. However, the presence of distractors in the cued as well as the irrelevant field only seemed to modulate early visual processing following stimulus presentation, but did not involve activity outside of visual areas.

ERP components related to (failed) distractor filtering

Contrary to our predictions, time-frequency analyses did not reveal any distractor filtering-related modulations of (alpha) oscillatory power during VSTM retention. Yet, previous ERP studies have shown robust effects of distractors presented among targets in the relevant hemifield on ERP components related to distractor storage (the CDA) and distractor signaling (the frontal bias signal; Liesefeld et al., 2014; Vogel et al., 2005). We therefore examined if we could replicate these findings and observe ERP correlates of (failed) distractor filtering.

The amplitude of the CDA scaled with the number of to be remembered items ($F_{2,60} = 8.41$; $p < .01$), but leveled off at VSTM capacity (cf., e.g., Vogel & Machizawa, 2004)

(Figure 5B). Moreover, in line with previous reports (e.g., Liesefeld et al., 2014; Vogel et al., 2005), VSTM capacity predicted the extent to which distractors were prevented from being stored in VSTM across individuals, as indicated by a trend towards a negative relationship between individual VSTM capacity and the effect of distractors on CDA amplitude, both for the effect of two distractors (2T0D vs. 2T2D; $r_{29} = -.26$, $p = .076$; see Figure 5C), as well as for the effect of four distractors (2T0D vs. 2T4D; $r_{29} = -.28$, $p = .061$). Repeating this analysis with the estimate of VSTM capacity used in previous research (Cowan's K instead of Pashler's K), yielded similar results ($r_{29} = -.28$, $p = .065$ for 2T0D vs. 2T2D; $r_{29} = -.27$, $p = .075$ for 2T0D vs. 2T4D).

Replicating previous findings (Liesefeld et al., 2014), we observed a distractor-sensitive frontal bias signal centered on electrode AFz (incorporating F1, F3, AF3, Fz, AFz, AF4, F4, and F2; see Figure 5D), with a peak between 240 and 290 ms after stimulus presentation, of which its amplitude differed between conditions with and without distractors ($t_{30} = 2.18$, $p = .037$; see Figure 5E). Moreover, further in line with previous findings, we found a negative cross-subject correlation between the amplitude of this frontal distractor detection signal and unnecessary storage of distractor stimuli, as reflected in distractor-related amplitude of the CDA and frontal bias signal (2T0D vs. 2T2D; $r_{29} = -.45$, $p = .006$; see Figure 5F). Thus, our ERP analyses confirmed that participants did recruit reactive filtering mechanisms in response to the presence of irrelevant distractor stimuli in our study.

Discussion

In this EEG study, we examined the functional characteristics and neural mechanisms of proactive and reactive distractor filtering. Behaviorally, distractors presented among targets in the relevant hemifield impaired VTSM performance, but distractors in the irrelevant hemifield did not. As the presence of distractors in the irrelevant hemifield could be predicted, it is possible that proactive suppression of information processing in the irrelevant hemifield prevented them from influencing target encoding. Indeed, time-frequency analysis of our EEG data showed that anticipated distraction was accompanied by alpha modulations over lateral occipital areas, with stronger alpha activity over the hemisphere processing distractors compared to the hemisphere processing the targets (prestimulus alpha lateralization). Also, the degree of proactive distractor suppression (measured as pre-stimulus alpha lateralization) was not related to the effect of subsequent distractors in the irrelevant hemifield on behavior across individuals, possibly suggesting that subjects were generally well capable of preventing irrelevant-hemifield distractors from influencing task performance. Furthermore, and in contrast to our prediction, we did not observe a reactive adjustment of alpha lateralization that scaled with the number of distractors in the irrelevant hemifield, in contrast to earlier findings reported by Sauseng et al. (2009). One explanation for this discrepancy in findings is that in our study, subjects had more time (700 ms after cue onset) to proactively prepare for upcoming distraction compared to the study by Sauseng et al., in which the stimulus display almost immediately followed the attentional cue (200 ms after cue onset). Thus, in our study, proactive filtering of distractors presented at an irrelevant location was associated with a distractor load-independent lateralization in alpha band activity both in the pre-stimulus interval and during VSTM retention. This may suggest that alpha activity in sensory cortices primarily serves to tune the brain towards processing of goal-relevant information, and thereby impedes encoding of anticipated irrelevant information into VSTM even when distractor load is high.

While distractors in the irrelevant hemifield had no effect on VSTM performance, distractors in the relevant hemifield did impair VSTM performance. Moreover, the degree to which these distractors impaired performance was related to individuals' VSTM capacity. Our ERP data mirrored these behavioral findings: we observed a prefrontal filter signal, which determined subsequent unnecessary parietal storage of distracting information, as indicated by the amplitude of the CDA. While the ERP data clearly revealed the presence of within-hemifield distractor filtering mechanisms, using time-frequency analyses, we could not find evidence for oscillatory power modulations involved in within-hemifield distractor filtering, even when taken a data-driven single-trial regression approach. This analysis revealed that while early contralateral theta activity scaled with the number of distractors in the cued hemifield, it similarly scaled with the number of targets in the cued visual hemifield, arguing against an interpretation of this activity as a distractor-selective mechanism. Based on these results, we conclude that although participants clearly tried to selectively encode the relevant information into VSTM, as indicated by our behavioral and ERP findings, selective filtering of irrelevant information is not evidently reflected in power modulations of low-frequency cortical oscillatory activity. Strikingly, a recent EEG study by Noonan et al. (2016) on the neural mechanisms involved in attentional modulation of target and distractor processing, also found no evidence for a role for alpha oscillations in distractor suppression, even though their ERP and behavioral findings showed evidence of distractor suppression. Furthermore, the absence of reactive alpha power modulations by unanticipated distractors in our study is in line with recent studies showing that in the absence of distractors, alpha power modulations bias sensory activity prior to anticipated goal-relevant events, but do not play a role during subsequent sensory processing of information (Bauer, Stenner, Friston, & Dolan, 2014; van Ede, Szebényi, & Maris, 2014).

These and our findings suggest that alpha power modulations may not unequivocally be involved in reactive distractor suppression.

We investigated reactive distractor filtering using targets and distractors that were spaced closely together in the cued hemifield, resembling distraction in more realistic situations (Peelen & Kastner, 2014). However, this may have two potentially problematic consequences. First, the distractor and target stimuli may have been processed in (partially) overlapping receptive fields (Kastner & Ungerleider, 2001), preventing or complicating selective modulation of distractor processing. Secondly, smearing of oscillatory brain activity at the level of the scalp may have masked possible focal effects of processing of target and distractor stimuli. Yet, this issue would likely be most influential in sensory cortex, where initial processing of the targets and distractors may take place in a retinotopic fashion. Moreover, our ERP findings indicate that we were able to capture distractor-dependent changes in cortical activity using our experimental paradigm. Yet, it is important to establish whether distractor-related local modulations of alpha power can be detected using electrophysiological methods characterized by a higher spatial resolution, such as electrocorticography (cf., de Pesters et al., 2016; Harvey et al., 2013).

Another consideration is that our mixed design (in which trials with and without distractors were randomly intermixed in a block) may have generated ambiguity about the actual presence and precise number of within-hemifield distractors across trials. It has recently been shown that people become less efficient in filtering of distractors when they need to switch between different filter settings across trials (Jost & Mayr, 2016; Noonan et al., 2016). The need to flexibly adjust filter settings on each trial may thus have caused participants to adopt a more cautious, filter-like strategy across trials, regardless of the presence and precise number of distractors in the cued hemifield (see also Marini, Demeter, Roberts, Chelazzi, & Woldorff, 2016; Marini, Chelazzi, & Maravita, 2013). Yet, this leaves unexplained why we did observe clear effects of distractors on ERP components and VSTM performance. Future studies are necessary to elucidate the possible differential effects of blocked vs. mixed presentation of distractor-present and distractor-absent trials on distractor filtering and associated oscillatory mechanisms. Nonetheless, our current findings indicate that in situations in which (the amount of) distraction is not always fully predictable, alpha oscillatory power is not involved in reactive distractor suppression.

Note that it is possible that distractors affected oscillatory dynamics that were not investigated in the present study, as we only looked at oscillatory power. Perhaps within-hemifield distractor filtering is more robustly reflected in other indices of neural oscillatory activity such as long-distance phase synchronization, which has been suggested to play an important role in top-down attention (Siegel, Donner, Oostenveld, Fries, & Engel, 2008; Womelsdorf & Fries, 2007). VSTM retention and top-down attentional control have specifically been shown to be subserved by interregional phase synchronization of alpha and beta band activity (e.g., Palva, Monto, Kulashekhar, & Palva, 2010; Zanto & Gazzaley, 2009; Womelsdorf & Everling, 2015). Furthermore, there is evidence for the involvement of phase-amplitude coupling in attentional modulation of sensory processing: coupling of gamma power to the phase of alpha oscillations results in rhythmic inhibition of sensory processing (Bonnefond & Jensen, 2015; Jensen, Gips, Bergmann, & Bonnefond, 2014). The potential role of interregional phase synchronization as well as phase-amplitude coupling in reactive suppression of irrelevant information needs further attention.

Nonetheless, it is intriguing that we did not observe any power modulations associated with of reactive distractor filtering, in particular given that we did observe effects of distracting information on VSTM performance and ERP indices related to filtering and VSTM storage. We conclude that reactive filtering of distracting information during VSTM retention may not rely on local modulations of occipital alpha oscillatory power.

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CHAPTER 3

Spatiotemporal dynamics of attention during visual short-term memory

Selective attention is a key predictor of efficient information storage in visual short-term memory (VSTM). Yet, the spatiotemporal characteristics of attention during VSTM, especially during post-perceptual stages following encoding and under conditions of high memory load, remain presently unclear. In the current study, we investigated the spatiotemporal dynamics of attention during VSTM encoding and maintenance. Participants performed a change detection task with varying memory load (six or three items). Attentional deployment to different locations was tracked continuously by means of Steady-State Visual Evoked Potentials (SSVEPs), using unique frequency tags for every location. We found that when memory load was within capacity (three items), spatiotemporal dynamics of SSVEP responses at to-be-remembered relevant locations were significantly different from irrelevant locations. Attentional modulation of SSVEP amplitude was spatially selective to relevant but not irrelevant locations in the display. The observed attentional modulations commenced during encoding, and importantly, continued during VSTM maintenance. Moreover, during encoding, they also predicted individual working memory-capacity across subjects. Lastly, analyses of the temporal dynamics of attentional deployment to individual stimulus locations provide tentative evidence for sequential rehearsal of information across locations during VSTM maintenance, suggesting that previously documented rhythmic sampling during perceptual monitoring may extend to VSTM retention. Together, these findings corroborate an important role of spatial attention in encoding as well as maintenance of information stored in VSTM, and provide preliminary support for sequential attentional sampling of to-be-remembered locations. Our findings also illustrate the usefulness of SSVEPs for continuously tracking attention to as many as six individual locations during VSTM.

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Introduction

The importance of selective attention for encoding goal-relevant information in visual short-term memory (VSTM) is widely acknowledged (Awh, Vogel, & Oh, 2006; Gazzaley & Nobre, 2012; Shipstead, Harrison, & Engle, 2015). Specifically, attention filters information before it enters VSTM to ensure selective storage of goal-relevant information in VSTM (Gazzaley, 2011; Peterson et al., 2014; Vogel & Awh, 2008; Vogel, McCollough, & Machizawa, 2005). Yet, the extent to which attention is also involved in subsequent maintenance and protection of information in VSTM is less clear.

According to the influential 'attention-based rehearsal' hypothesis, attention serves to keep representations active during VSTM maintenance (Awh et al., 1998; Awh & Jonides, 2001). This account is supported by findings showing impaired memory performance when spatial attention is directed away from to-be-remembered locations during VSTM maintenance (e.g., Awh et al., 1998; Smyth & Scholey, 1994; but see also Belopolsky & Theeuwes, 2009), and enhanced sensory processing of information presented at to-be-remembered locations during VSTM maintenance (Awh, Anllo-Vento, & Hillyard, 2000; Fukuda & Vogel, 2009). Another key result supporting the attention-based rehearsal account is the observation of activity in highly overlapping brain networks during spatial attention and VSTM maintenance (Awh, Vogel, & Oh, 2006; Postle, Awh, Jonides, Smith, & D'Esposito, 2004), suggesting that sustained representation-specific activity during VSTM maintenance may form the neural basis of attention-based rehearsal.

Previous research on the role of attention in VSTM, however, leaves unresolved whether attention-based rehearsal also occurs when VSTM is fully loaded, or contains more complex representations. Support for the notion of attention-based rehearsal during VSTM so far comes from experimental paradigms in which only one or two (greatly distinct) items had to be remembered (Awh et al., 1999; Postle et al., 2004; Sprague, Ester, & Serences, 2016; Towler, Kelly, & Eimer, 2015). Yet, maintenance of goal-relevant information in everyday life demands storage of many similar and often complex visual representations (e.g., Brady, Störmer, & Alvarez, 2016; Orhan & Jacobs, 2014; Peelen & Kastner, 2014). Existing approaches preclude any conclusions about the scope of attentional deployment across multiple locations during VSTM when memory load is high.

Another unresolved issue concerns the temporal dynamics of attention during VSTM. Intriguing recent findings indicate that the spatial and temporal dynamics of attentional control are intrinsically related. Contrary to the long prevailing conception of attention as a multifocal spotlight that simultaneously supervises non-adjacent locations

(Malinowski, Fuchs, & Müller, 2007; Muller, Bartelt, Donner, Villringer, & Brandt, 2003), recent studies indicate that attention may sequentially sample information across different locations in a rhythmic fashion (VanRullen, 2016). Specifically, when observers monitor multiple locations, fluctuations in visual detection performance at individual locations reveal a rhythmic, anti-phase pattern across locations (Dugué, McLelland, Lajous, & VanRullen, 2015; Fiebelkorn, Saalmann, & Kastner, 2013; Landau & Fries, 2012; Landau, Schreyer, Van Pelt, & Fries, 2015), indicative of sequential attentional sampling across locations. Similarly, VSTM maintenance has been proposed to rely on a periodic reactivation of stored representations (Barrouillet & Camos, 2012; Van Vugt, Chakravarthi, & Lachaux, 2014). Empirical support for serial reactivation of stored representations in VSTM is currently limited to studies using indirect measures such as retrocues to probe attention to stored representations (Souza, Rerko, & Oberauer, 2015). Retrocues, which instruct subjects to perform attentional manipulations on stored representations during maintenance, may not only interfere with ongoing VSTM, but also introduce additional attentional modulations into the task that are not necessarily inherent to VSTM.

In the current EEG study, we sought to measure the spatiotemporal dynamics of attention during VSTM more directly. Hereto, we simultaneously tracked attentional allocation during VSTM to multiple (i.e., six) stimulus locations that could be task-relevant (containing to-be-remembered stimuli) or task-irrelevant. Attention was measured by means of steady-state visual evoked potentials (SSVEPs) elicited by unique frequency tags at each stimulus location. Our approach was thus characterized by a high spatial and high temporal resolution, which permitted us to address three specific outstanding questions. First, we examined whether the effects spatial of attention during VSTM encoding persists during VSTM maintenance. Do we see similar modulations of internal sensory representations as during encoding? Secondly, we assessed the functional relevance of observed attentional modulations for VSTM performance. Based on the attention-based rehearsal account (Awh & Jonides, 2001), we expected to find attentional modulation of sensory representations during VSTM maintenance that would be predictive of VSTM performance across individuals. Third, we explored the temporal characteristics of spatial attention to individual locations during VSTM, and specifically tested the notion of sequential rehearsal of to-be-remembered stimulus locations by means of lagged cross-correlations of SSVEP amplitude envelopes.

Methods

Participants

Twenty-eight participants were recruited using the online participant recruitment system of the University of Amsterdam. All participants were neuropsychologically healthy (assessed based on self-report), right-handed, and were screened on color blindness, migraine and epilepsy. Participants provided informed consent before participation, and received monetary compensation or research credits for their participation in the experiment. The experimental procedure was in accordance with the local institutional guidelines, and was approved by the local ethics committee of the University of Amsterdam. As specified below, our final sample used for the analyses consisted of 21 participants (M = 21.7 years (range 18-32 years); 18 F).

Experimental task

Participants performed a visuo-spatial change detection task with varying memory load that was adapted to allow measurement of spatial attention to six stimulus locations. Memory load on the task was manipulated block-wise, and alternated between three items (close to average VSTM capacity) and six items (exceeding average VSTM capacity; Luck & Vogel, 2013). Stimulus presentation and response registration were controlled using Psychtoolbox (Brainard, 1997) and Matlab (The MathWorks). Stimuli were displayed on a 24-inch monitor with a 144 Hz refresh rate. Stimuli were presented on square placeholders (width/height 1.2 dva), positioned on a ring around fixation (center at 4 dva from fixation). Memory items were simple geometric shapes (.9/1.02 dva diameter; squares/circles; counterbalanced across participants) with different, highly distinguishable colors of comparable luminance (red; orange; purple; blue; turquoise; green; yellow; maximal luminance difference of 10 cd/m2). In the low memory load condition, memory items were assigned to stimulus locations in a pseudorandom fashion and were always placed on three placeholders distributed across both hemifields. Participants were asked to remember the color of all the stimuli presented in the memory display at each location.

Placeholders at stimulus locations changed luminance from black to white in a sinusoidal fashion with different tagging frequencies for each location (see Figure 1a-b), resulting in six location-specific SSVEPs on every trial. Each trial started with a 1000 ms presentation of six flickering placeholders in order to initialize entrainment of an SSVEP response to the flickering placeholders (Gulbinaite, Johnson, de Jong, Morey, & van Rijn, 2014; see Figure 1a). Tagging frequencies were selected such that they would not interfere with induced activity in the frequency range of activity that is usually observed during VSTM, such as theta (4-8 Hz), alpha (8-12 Hz), and gamma (30-80 Hz) activity (Roux & Uhlhaas, 2014; Vissers, van Driel, & Slagter, 2016). The tagging frequencies ranged from 13 to 24 Hz and were chosen such that each cycle covered an integer number of screen refreshes on 144 Hz monitor (13.0909, 14.4, 16, 18, 20.5714 and 24 Hz). On high load trials, tagging frequencies were randomly assigned to stimulus locations. On low load trials, frequencies were pseudo-randomly assigned to stimulus locations, such that the frequencies assigned to relevant locations were selected from the array of possible tagging frequencies in a stacked manner. Here, odd or even entries in the array with possible frequencies were assigned to the relevant locations (e.g., 13.0909; 16; 20.5714 Hz flickering placeholders at relevant locations and 14.4; 18; 24 Hz at irrelevant locations or vice versa; odd and even entries were counterbalanced within the low load condition). This way, relevant and irrelevant positions on low load trials were always assigned a comparable range of tagging frequencies.

After a maintenance interval of 2000 ms, the placeholders stopped flickering and one of the target stimulus locations was probed. Participants were asked to indicate whether the probe color was same or different with respect to the memory stimulus at that particular location by pressing one of two buttons attached to the right armrest of the chair (right index finger for ‘change’; right middle finger for ‘no change’). The probe stimulus was presented at a randomly selected target location. On half of the trials the probe color was different from the color of the target presented at that location in the memory display (change trial), on the other half of trials the probe color was identical (no-change trial).

To ensure that participants bound stimulus colors to stimulus locations, we manipulated the color of the probe stimulus such that on half of the change trials the probe color was identical to the color of a stimulus at a non-probed target location (‘lure trials’). On the other half of change trials, the probe would adopt a ‘new’ color (‘new change trials’; see Figure 1a). Binding of stimulus color to location would result in an equal performance on lure and new change trials, whereas a lack of color-location binding (e.g., if participants would simply verbalize target colors) should result in impaired performance on lure trials. This manipulation thus enabled to assess the degree to which participants bound stimulus color to location during VSTM. Lure and new change trials were randomly interspersed among no-change trials. After a response was made or when the response interval (1000 ms) elapsed, the placeholders were removed from the screen. An inter trial interval (ITI) of 1000 ms preceded the next trial.

The experiment consisted of 6 blocks of 64 trials adding up to a total of 384 trials. Memory load was manipulated block-wise and alternated across blocks. The memory load condition (low vs. high) with which the experiment would start was counterbalanced across participants. Participants were allowed a self-paced break every 32 trials, during which their average reaction times and accuracy levels across the past 32 trials were presented on the screen to keep them motivated during the course of the task.

Throughout the entire experiment, eye movements were monitored using a Tobii eye tracker (Tobii AB, Stockholm, Sweden). Gaze data were analyzed online, so that the experimenter could remind the participant to keep fixation in case the participant repeatedly broke fixation during trials.

Procedure

Participants were seated at a 90 cm distance from the computer monitor and were given extensive task instructions. They performed a practice session consisting of four practice blocks of 16 trials each. In the first two practice blocks, immediate feedback was given on participants' performance ('correct', 'incorrect' or 'too late'). In the last two practice blocks there was no trial-wise feedback anymore, similar to the experimental task. After the practice session, participants continued with the change-detection task. Subsequently, participants performed a short contrast-detection task. Data from this task were collected for other purposes and will not be presented or discussed here.

In total, the EEG session lasted approximately one hour. At the end of the EEG-session, participants were invited for a separate short behavioral session in which we administered a symmetry span task (Unsworth, Heitz, Schrock, & Engle, 2005), to obtain an independent index of participants' visual working memory capacity (Conway, Kane, & Al, 2005).

EEG recording, pre-processing and electrode selection

EEG-data were sampled at 512 Hz using a Biosemi set-up, with 64 channels placed according to the international 10-20 system. External reference electrodes were placed at the earlobes, to be used for off-line referencing of the data. External electrodes placed above and below the left eye were used to measure vertical eye movements and blinks (VEOG), and electrodes placed at the outer canthi were used to measure horizontal eye movements (HEOG).

Off-line, the EEG data were high-passed filtered at 0.5 Hz, and epoched from -2200 to 5000 ms around onset of presentation of the memory display. The epoched dataset was manually inspected and trials with large muscle artifacts, as well as blinks during presentation of the flickering placeholders (potentially impeding the entrainment of the SSVEP), were excluded from further analysis. Lastly, the gaze data measured with the eye tracker were used to detect and reject trials containing eye-movements during the encoding and maintenance interval of the task (≥ 1.5° visual angle away from fixation

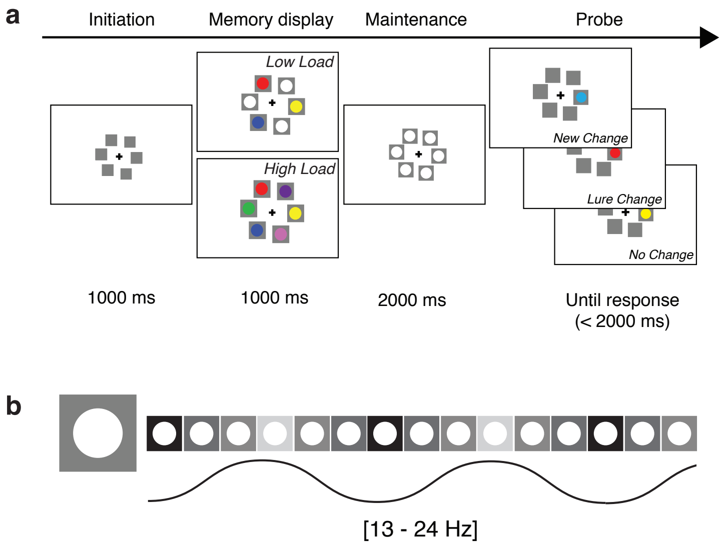

Figure 1. Graphical display of the change-detection task. A) In a trial, participants were shown a memory display with three (low memory load; top panel) or six (high memory load; bottom panel) targets. Memory load was manipulated block-wise. Probe displays would contain a probe stimulus that would either have a new color (new change trials; top panel), would have a color of one of the target stimuli at a non-probed location (lure trials; middle panel), or was identical to the target stimulus at that location (no change; bottom panel). B) Stimulus contrast of the placeholders at stimulus locations was manipulated in a sinusoidal fashion from black to white to elicit SSVEPs. Six tagging frequencies ranged from 13 to 24 Hz.

for ≥ 50 consecutive ms). Following this procedure, the datasets contained 346.9 trials (90 % of the total number of trials in the experiment) on average (SD=15.7; 4.1 %).

SSVEP analyses: spatiotemporal filtering

The SSVEP and ongoing spontaneous oscillatory activity usually have overlapping frequency content, impeding separation of the SSVEP based on spectral characteristics of the data alone. In order to optimally extract SSVEPs, we exploited spatiotemporal characteristics of the SSVEP signal (frequency and scalp distribution). This was done through rhythmic entrainment source separation (RESS) (Cohen & Gulbinaite, 2017). RESS belongs to a family of denoising source separation techniques that can be optimized to extract specific spatiotemporal features of the data (Jaakko, Särelä, & Varela, 2005). RESS comprises the computation of a spatial filter that effectively maximizes the explained variance for a specified feature of the data, in our case the frequency-specific SSVEP signal, relative to a reference signal, in our case ongoing electrophysiological activity at frequencies closely neighboring the SSVEP frequencies of interest. RESS was performed on the concatenated epochs spanning the time window during which the flickering stimuli were presented on the screen (excluding the first 500 ms during which the SSVEP was still building up, resulting in a window of -500 to 3000 ms around stimulus presentation). Power at the SSVEP frequency was isolated by band-pass filtering the concatenated trials using a narrow-band filter centered at the SSVEP frequency of interest (frequency-domain Gaussian filter kernel; FWHM = 0.5 Hz). The bandpass filtered EEG data at neighboring frequencies of each SSVEP frequency (± 2 Hz; FWHM = 1 Hz) was averaged across neighboring frequencies and taken as the reference data. Time-averaged covariance matrices were computed separately for the SSVEP data at the center frequency (S) and the reference data (R). Generalized eigenvalue decomposition of the matrix product $R^{-1}S$ was used to construct tagging frequency-specific spatial filters (RESS components). The eigenvector (i.e., channel weights) with the largest eigenvalue was selected as the spatiotemporal filter at the tagging frequency. This eigenvector (column vector with values representing channel weights) was multiplied by the original channel time series to obtain a component time series. As can be seen in Figure 3c, the frequency content of the resulting component time series is highly specific to the tagging frequencies used.

Given that topographies of SSVEPs may differ across participants and frequencies (Gulbinaite et al., 2014), we computed the spatial filters separately for each participant and flicker frequency. Furthermore, as activity elicited at different stimulus positions may project differently onto the scalp (Vanegas, Blangero, & Kelly, 2015), the procedure described above was performed separately for each subset of trials on which a frequency was presented at the same stimulus position (see Figure 3a). This finally resulted in six frequency-specific component time courses optimized for each flicker frequency (see Figure 3b) and trial-specific stimulus configuration on the display. Note that construction of the spatial filters was done on the condition-average data (collapsed across locations and memory load), and was thus independent of potential effects of experimental manipulations.

As the main potential danger of RESS is overfitting (Cohen & Gulbinaite, 2017), resulting in time series reflecting noise instead of SSVEPs, we only included participants for whom inspection of frequency spectrum of the raw data showed a peak for more than three of the six SSVEP frequencies on at least one of the 16 most posterior channels. Furthermore, we excluded the most anterior channels (Fpz; Fp1-2; AF3-4; AF7-8; FC3-4; FC5-6; F3-4; F5-6; F7-8; FT7-8; T7-8) prior to RESS to prevent contamination of the component time series by frontal electromyographic (EMG) artifacts at the frequency of interest. RESS was performed using the 43 remaining channels (see Figure 3a-b).

The effect of experimental manipulations on SSVEP amplitude was assessed by comparing the SSVEP response across experimental conditions (low vs. high memory load; stimulus vs. empty locations) and time intervals (encoding (0-1000 ms);

maintenance (1000-3000 ms)). Hereto, we performed an FFT on the single-trial data, and computed the trial-average frequency spectrum for every condition (the data was zero-padded to achieve a frequency resolution of .01 Hz). In order to avoid an effect of power-law scaling of EEG data on our results, we expressed the power at each flicker frequency as signal-to-noise-ratio (SNR), which was computed as the power at the SSVEP peak relative to the power at neighboring frequencies (Δf at ± .5 Hz and ± .75 Hz; Nikulin, Nolte, & Curio, 2011). In the following, whenever we mention SSVEP response, we refer to the SNR of the SSVEP computed as outlined here.

We also explored whether fluctuations in attentional deployment to individual locations would support the notion of sequential attentional deployment across different locations. The temporal relationship between attentional allocation to different stimulus locations was assessed using lagged correlations (VanRullen & MacDonald, 2012), with power modulations of the SSVEP response at individual stimulus locations reflecting attention to a particular location. Analyses were based on correct trials in the low memory load condition only. As the cross-correlation reflects the similarity between two (lagged) time series, we used two locations on each trial to compute the cross-correlation. Specifically, we used SSVEPs corresponding to two stimulus locations presented in the same hemifield (note that on each low load trial, there were always only two locations presented in one hemifield), also because previous research has revealed potentially different temporal characteristics of sampling across (objects in) different hemifields (Cavanagh & Alvarez, 2005; Fiebelkorn et al., 2013; Landau & Fries, 2012; Strong & Alvarez, 2016). We examined whether the resulting patterns of cross-correlation of attentional deployment to within-hemifield locations would be in stronger support of sequential or parallel attentional deployment across locations. Sequential or rhythmic attentional allocation to stored representations should result in significant cross-correlation at non-zero time-lags (see Figure 6a), whereas parallel attentional modulation across stimulus representations should result a high cross-correlation at time-lag zero followed by a steep drop in the cross-correlation for lagged versions of the signal (see Figure 6b). All analyses were repeated for irrelevant (empty) locations to be able to compare the temporal dynamics of attentional allocation to relevant and irrelevant locations.

In order to quantify the temporal dynamics of attention at two locations on every trial, we first computed time-varying fluctuations of SSVEP power. This was done by band-pass filtering the RESS time courses at the SSVEP frequency of interest (FWHM = 4 Hz; Cohen & Gulbinaite, 2017), and extracting the magnitude of the Hilbert transform of the band-pass filtered time course to obtain a power envelope reflecting SSVEP power modulations over time. Power envelopes were used for subsequent cross-correlation analyses to assess the temporal relationship between attentional modulations of different representations (VanRullen & MacDonald, 2012).

Power envelopes were entered in the cross-correlation using time points corresponding to the task intervals (separately for encoding (0-1000 ms) and maintenance (1000-3000 ms)). Cross-correlations were computed for all possible lags (e.g., -1000 to 1000 ms in steps of 1.953 ms (samples) for the encoding interval of 1000 ms) by moving the power envelope of the SSVEP for one location along the power envelope of the SSVEP at another location, and multiplying the two signals. The cross-correlation between two locations was computed at the single-trial level, after which the lagged correlations were averaged across trials. The trial average cross-correlations for every subject were used for group-level analyses. Cross-correlations were performed using within-hemifield pairs of stimulus and irrelevant locations separately.

Statistical analyses

Behavioral data were analyzed after removal of trials on which participants made eye movements (see EEG preprocessing for details), and after removal of response omissions and fast, uninformed responses (RT < 150 ms). The effects of memory load (three vs. six items) and trial type (no change; lure change; new change) on accuracy (% correct) and speed (RT in ms) of performance were assessed using separate repeated measures ANOVAs. Significant effects were assessed with follow-up contrasts. In order to assess color-location binding, we used planned comparisons to test the difference in performance on lure-change vs. new-change trials. VSTM capacity was defined using Cowan's K (K_c) using the equation K_c = (H-FA)*N, where H represents the hit rate, FA the false alarm rate, and N the set size (3 vs. 6). VSTM capacity was obtained by selecting the maximum value of K_c across memory loads (Cowan, 2001). Working memory capacity (WMC) was measured as the partial symmetry span score on the symmetry span task (Conway et al., 2005).

In order to determine whether participants allocated more attention to relevant compared to irrelevant locations during VSTM maintenance and encoding, we averaged SSVEP power at relevant (stimulus) and irrelevant (empty) locations on low load trials. Here, we collapsed across individual tagging frequencies based on stimulus presence. SSVEP responses were subjected to a repeated measures ANOVA with the within-subject factors interval (encoding; maintenance) and location (relevant; irrelevant location). In order to establish whether attentional allocation during VSTM was related to individual differences in VSTM performance, we correlated the attention effect (operationalized as the difference in SSVEP power at relevant vs. irrelevant locations on low load trials) with VSTM capacity (K_c) during VSTM encoding or maintenance (using Spearman's correlation coefficient). In order to assess whether attentional allocation during VSTM maintenance was functionally relevant, we compared SSVEP power during maintenance at the probed location on correct vs. incorrect trials using an ANOVA with accuracy (correct vs. incorrect) and memory load (low vs. high) as within-subject factors (one participant who did not make errors in one of the conditions was excluded from these analyses). Significance of the cross-correlations between SSVEP envelopes was tested against 0 (reflecting no temporal relationship between the time courses). Trial-average cross-correlations at relevant (stimulus) and irrelevant locations were also compared directly, to test for possible differences in the spatiotemporal dynamics of attention to relevant vs. irrelevant locations. The cross-correlation analyses were repeated separately for locations presented in the left and right hemifield, in order to establish whether the observed pattern in the aggregate data would replicate for the separate hemifields (Landau & Fries, 2012). An alpha level of .05 was used as the significance criterion for all statistical analyses.

Results

Participants

Twenty-eight participants took part in the experiment. Two participants were excluded because of poor performance (at or near chance performance (~50% correct) in the low load condition). Three additional participants were removed because of a low number of artifact-free trials in the EEG data (more than 50% of the trials contained muscle or eye-blink artifacts). Finally, two participants were excluded because their SSVEPs at posterior scalp sites were not distinguishable from noise (see the Methods section for details). Our final sample consisted of 21 participants (M = 21.7 years, SD = 3.1; age range 18-32, 18 females).

VSTM performance

As can be seen in Figure 2a-b, and as predicted, VSTM performance was affected by memory load ($F_{1,20} = 118.70$, $p < .001$; see Figure 2a): Performance was more accurate on low (M = 86%) compared to high (M = 71%) memory load trials ($t_{20} = 10.90$, $p < .001$). The main effect of trial type was also significant ($F_{2.0,23.9} = 10.67$, $p < .01$), reflecting that performance was significantly lower on no-change trials (M = 68%) compared to new change trials (M = 86%; $t_{20} = -4.45$, $p < .001$), as well as lure change trials (M = 81%; $t_{20} = -3.30$; $p < .01$). Importantly, performance accuracy on the new and lure change trials was not significantly different ($t_{20} = 1.16$, $p = .486$), indicating that, in general, participants bound stimulus color to location, i.e., remembered stimulus colors at specific locations. The interaction between memory load and trial type was also significant ($F_{1.4,29.0}$ = 5.99, *p* = .012), indicating that the effect of memory load was not identical across trial types. Post-hoc analyses showed that performance was more reduced under high compared to low memory load in no-change trials compared lure change (t_{20} = 3.05; *p* = .006) or new change trials (t_{20} = 1.98; *p* = .062). Memory load did not differentially affect accuracy of performance on new and lure change trials (*p* = .105). Thus, in the high compared to the low-load condition, participants performed less well at remembering if the probe color was the same as the previously presented target at that location, particularly when the probe color had not changed.

Mean accuracy level was 71% correct in the high load condition, suggesting that many participants had trouble remembering 6 items (chance level was 50% correct). Indeed, average VSTM capacity (K_c) was 2.3 items (M = 2.34; SD = .64), which is well below the six items that had to be remembered in the high memory load condition. Relatedly, complex working memory capacity (as estimated using the symmetry span task) was related to VSTM performance in the low load condition (see Figure 2c; r_{19} = .55, *p* = .010), but not in the high load condition (r_{19} = .29, *p* = .20). This indicates that our VSTM task reliably measured the ability to temporarily store information.

Reaction times were also affected by memory load ($F_{1,20}$ = 10.56, *p* = .004; Figure 2b). Responses were slower on high (M = 668 ms) compared to low (M = 633 ms) memory load trials (t_{20} = -3.25, *p* = .004). Trial type also affected reaction times ($F_{2,40}$

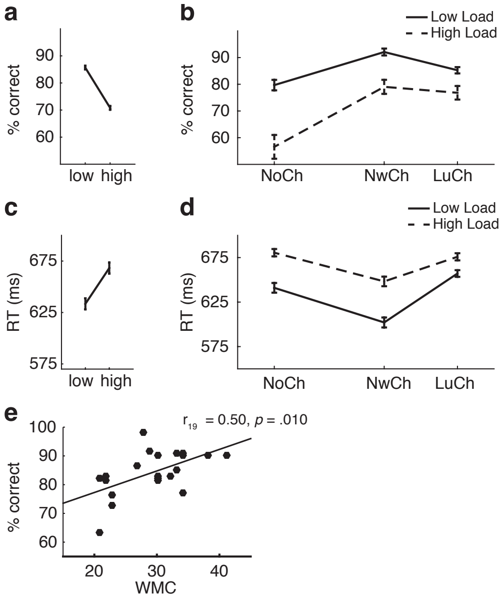

Figure 2. Effects of memory load and probe type on memory performance. A) Condition-specific accuracy of performance on the task, averaged across probe type. Participants performed worse under high load conditions. B) Accuracy levels per probe-type (no change; new change; lure change) and condition (low vs. high memory load). The interaction between memory load and probe type was significant, and reflected worse performance in the high load condition, in particular in no-change trials. C) Condition-specific response times on the task, averaged across probe type. Participants were also slower when memory load was high. D) Response times per probe-type (no change; new change; lure change) and condition (low vs. high memory load). Response times were significantly different across memory load, and the effect of memory interacted with the effect of probe type, such that the effect of memory load on response times were smaller on lure change trials compared to no change and new change trials. E). Working memory capacity (average performance on low and high memory load trials) was significantly correlated with accuracy on the change detection task in the low load condition.

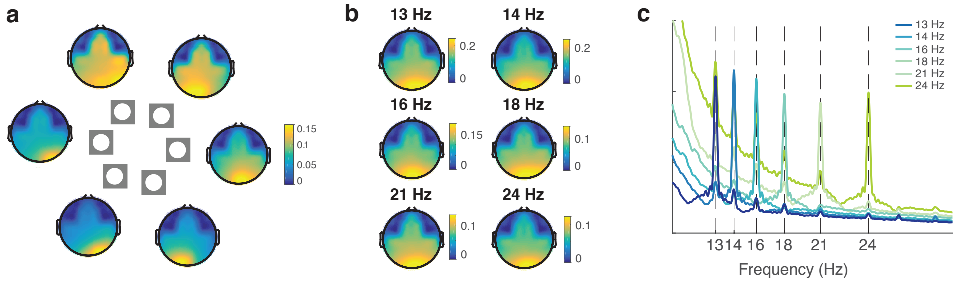

Figure 3. Topographical maps of SSVEP spatial filters of the Rhythmic Entrainment Source Separation (RESS) components and component frequency spectra. A) Condition-average topography of the RESS component time series (averaged over -500 to 3000 ms) separately displayed for the six individual stimulus locations. Color bars represent normalized channel weightings. B) Condition-average topography of the RESS component time series (averaged over -500 to 3000 ms) shown separately for the six frequencies used. Color bars represent normalized channel weightings. C) The frequency spectrum of the RESS component time series optimized for each SSVEP frequency. The frequency spectra show distinct differences between the six time series, and confirm that the content of the RESS component time series is highly specific to the corresponding SSVEP frequency.

= 23.28, $p < .001$). Post-hoc t-tests showed slower responses on lure (M = 667 ms) compared to new change trials (M = 625 ms; $t_{20} = 5.422$, $p < .001$), but no difference in speed of responding between lure and no-change trials (M = 661 ms; $p = .66$). Lastly, there was a significant interaction between the effects of memory load and trial type on speed of responding ($F_{2,40} = 3.97$, $p = .027$). Post-hoc comparisons showed that the difference in response speed between the high and low memory load conditions, was smaller on lure change compared to new change trials ($t_{20} = -2.52$; $p = .020$), and on lure change versus no-change trials ($t_{20} = -2.34$; $p = .030$). The effect of memory load on RT was not different between new change and no change trials ($t_{20} = -0.63$, $p = .534$). Thus, subjects performed worse in the high compared to the low memory load condition, and generally encoded stimulus color in a spatially specific way.

SSVEP analyses: Effect of stimulus relevance on spatial attention

Figure 4a summarizes frequency-specific SSVEP power results. To determine if attention not only modulates sensory processing during encoding, but also during maintenance, SSVEP responses at relevant and irrelevant locations (collapsed across tagging frequencies) were compared separately during the encoding and maintenance interval. A repeated measures ANOVA revealed a marginally significant effect of stimulus location on SSVEP power ($F_{1,20} = 3.496$, $p = .076$), indicating only weak attentional modulation of stimulus locations during VSTM. The main effect of interval was highly significant ($F_{1,20} = 115.07$, $p < .001$), with stronger SSVEP power during the maintenance (M = 3.21) than the encoding interval (M = 1.54, $t_{20} = 10.73$, $p < .001$).

This pattern conceivably reflects a stronger build-up of the SSVEP responses and/or an improved SNR during the longer maintenance interval compared to encoding (2000 vs. 1000 ms respectively). Notably, the interaction between interval and stimulus locations was highly significant ($F_{1,20}$ = 30.784, $p < .001$). As can be seen in Figure 4b, and confirmed by post-hoc comparisons, this interaction reflects significantly weaker SSVEP responses at relevant compared to irrelevant locations during encoding (t_{20} = -6.46, $p < .001$), but marginally significantly stronger SSVEP responses at relevant compared to irrelevant locations during maintenance (t_{20} = 2.051, p = .054). The observed weaker SSVEP responses at relevant vs. irrelevant locations during encoding

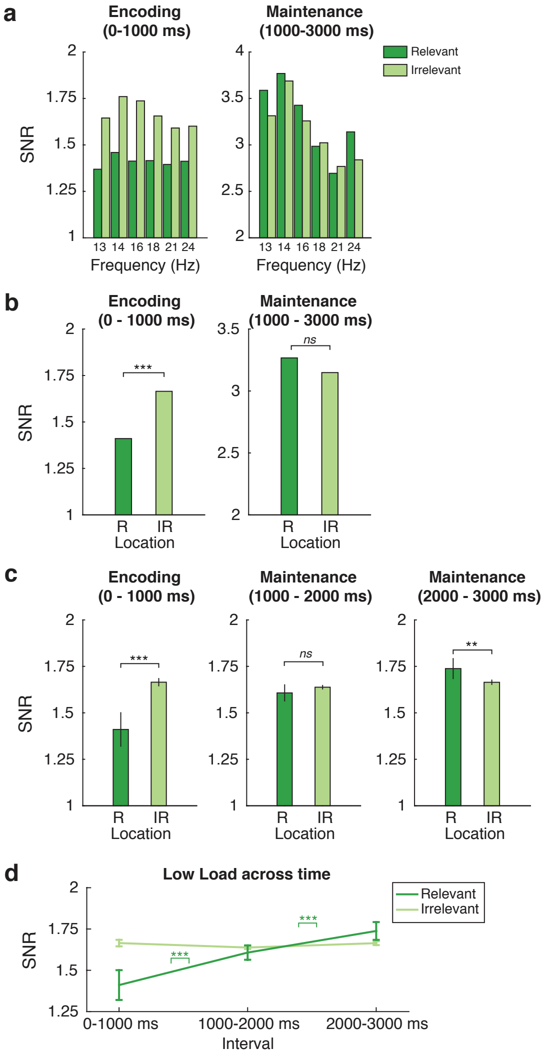

Figure 4. Attentional modulation of SSVEP responses during different stages of VSTM. A) SNR of the frequency-specific SSVEP response in the low load condition during the encoding (left panel) and maintenance interval (right panel), with the SNR of the SSVEP response at relevant locations depicted in dark green, and the SNR of the SSVEP response at irrelevant locations depicted in light green. This figure shows that the effects observed at the group level were not driven by a single frequency. B) SNR of SSVEP responses at relevant (dark green) and irrelevant (light green) locations, collapsed across SSVEP frequencies. SSVEP power was significantly lower at relevant compared to irrelevant locations during encoding, and marginally higher at relevant compared to irrelevant locations during maintenance. C) SNR of SSVEP responses at relevant (dark green) and irrelevant (light green) locations, separately for the first and second half of the VSTM maintenance intervals. This figure shows that during the second half of VSTM maintenance, SSVEP power was significantly higher at relevant vs. irrelevant locations. D) SSVEP power displayed for the encoding, early and late maintenance intervals (similar to 4C, but now visualized in order to emphasize the difference in temporal dynamics of attention to relevant compared to irrelevant locations). Clearly, attentional modulations of SSVEP power were selective to relevant locations, while SSVEP responses at irrelevant locations were not modulated by attention.

are particularly surprising given that attention is primarily thought to enhance sensory responses (Muller et al., 2003; Norcia, Appelbaum, Ales, Cottereau, & Rossion, 2015; Vialatte, Maurice, Dauwels, & Cichocki, 2010), but might be explained by suppression of the flickering placeholders surrounding the to-be-encoded stimuli during encoding (see Discussion). In this case, the observed flip in the direction of the attentional modulation from VSTM encoding to maintenance may suggest that during maintenance spatial attention broadened to include the placeholders, and furthermore raises the possibility that the first part of the maintenance interval was potentially 'contaminated' by the reversal of the direction of the attention effect, masking attentional modulation of sensory responses during VSTM maintenance. To establish whether this was the case, we repeated the analysis described above but now divided our maintenance interval into two equally long segments (1000 ms each; Figure 4c). This analysis again revealed a significant main effect of stimulus location ($F_{1,20} = 11.98$, $p = .002$), with lower SSVEP power at relevant locations (M = 1.58) compared to irrelevant locations (M = 1.66). The interaction between interval and stimulus location was again highly significant (F1.5,29.8 = 46.00, $p < .001$). As reported above, SSVEP power during VSTM encoding was significantly lower for relevant compared to irrelevant locations ($t_{20} = -6.46$, $p < .001$). As we suspected, this difference in SSVEP power disappeared during the first half of the maintenance interval ($t_{20} = -1.61$, $p = .122$), and flipped in sign during the second half of the maintenance interval ($t_{20} = 3.14$, $p < .01$). Importantly, these changes in SSVEP power across the different VSTM stages were in particular driven by changes in SSVEP amplitude at relevant locations (Figure 4d). That is, the SSVEP response elicited by flicker at relevant locations changed significantly over time ($t_{20} = -6.71$, $p < .001$ for encoding vs. first half of maintenance, $t_{20} = 5.91$, $p < .001$ for first vs. second half of maintenance), whereas the SSVEP response elicited by flicker at irrelevant locations did not significantly change across intervals (marginal effect for encoding vs. first half of maintenance; $t_{20} = 1.86$, $p < .077$; no effect for first vs. second half of the maintenance interval; $t_{20} = -1.71$, $p = .103$). These results indicate attentional modulation of relevant stimulus locations during VSTM encoding as well as maintenance, although the direction of attentional modulation changed across time.

SSVEP analyses: Individual differences in attentional allocation and VSTM capacity

In order to assess the relationship between VSTM capacity and attentional allocation during VSTM, we correlated the difference in SSVEP power for relevant compared to irrelevant locations on low load trials with VSTM capacity (K_c) during the time intervals during which we observed attentional modulations of SSVEP amplitude (encoding and late maintenance). Attentional allocation to relevant locations was not related to VSTM capacity during VSTM late maintenance across participants (r_{19} = .00; CI [-0.43, 0.43], *p* = .998) (Figure 5a). However, attentional modulation of stimulus locations during VSTM encoding was significantly related to VSTM capacity (r_{19} = .50, *p* = .02). Further inspection of the relationship shows that the unexpected direction of the attention effect during VSTM encoding (reduced amplitude of SSVEP responses for relevant vs. irrelevant locations) was present in participants with a low VSTM capacity, but less so participants with a high VSTM capacity (see Figure 5a). This finding suggests that there may be individual differences in attentional strategy during low and high VSTM capacity individuals used during encoding. Alternatively, different VSTM-capacity may have experienced a different degree of surround-suppression of the flickering placeholders. The present results do not allow us to infer the precise nature of the observed relationship. Yet, importantly, they reveal that individual differences in attentional deployment across stimulus locations during VSTM encoding, but not during VSTM maintenance, predicted individual differences in VSTM capacity.

To further determine if the observed attentional modulations are functionally relevant, we next investigated whether participants paid more attention to the probed location on correct compared to incorrect trials at different memory loads. Contrary to our expectation, an ANOVA with the factors memory load (low; high) and task interval (encoding; maintenance) revealed no effect of accuracy on the SSVEP response at the probed location ($F_{1,19}$ = 2.42, *p* = .136). Furthermore, we observed no interaction between the effects of accuracy of responding and the factors interval or memory load (all *p*'s > .85), suggesting that accuracy of responding was not associated with more attention to the probed location. Although the number of trials used to perform

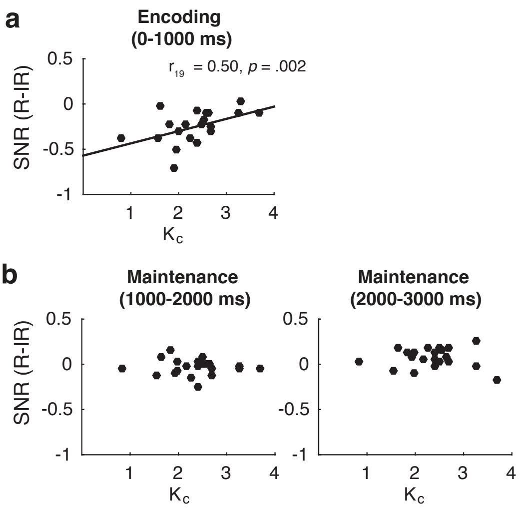

Figure 5. The functional role of spatial attention in VSTM. A) The relationship between attentional allocation (measured as the difference in SNR for SSVEPs at relevant and irrelevant locations) and VSTM capacity. There was a significant relationship between VSTM capacity and attentional allocation during VSTM encoding, but not during early and late VSTM maintenance. B) Attentional allocation to the probed locations on correct and incorrect trials. Attentional allocation to the probed location did not predict accuracy of performance on low or high load trials during any of the task intervals.

this analysis was relatively low (28.4 vs. 56.3 incorrect trials on low and high load trials respectively, averaged across participants), necessitating caution when interpreting these results, these findings do not support the notion that reduced SSVEP responses at the probed location resulted in impaired behavioral performance. Alternatively, attention during VSTM maintenance may not involve a sustained focus on multiple different locations, but may rather shift across stimulus locations in a sequential or rhythmic fashion (Busch & VanRullen, 2010; Dugué et al., 2015; Fiebelkorn et al., 2013). In this case, time average SSVEP responses may not be sensitive to a potential relationship between attention during VSTM maintenance and performance. We next explored the extent to which attention may have shifted across stored representations.

Exploratory analyses: temporal dynamics of attention during VSTM

Lastly, to explore if attention sequentially looped across relevant locations or not, we first analyzed the temporal dynamics of attentional deployment to two relevant and irrelevant locations presented within one hemifield (separately for relevant and irrelevant locations). We were particularly interested in the presence or absence of significant cross-correlations at nonzero time lags: The absence of significant cross-correlation at non-zero lags would be in support of a parallel attentional sampling process (see Figure 6b), whereas a significant cross-correlation at non-zero lags would be stronger support for sequential (and potentially rhythmic) attentional sampling or rehearsal (Figure 6a). During VSTM encoding, the cross-correlation of the SSVEP envelope to relevant and irrelevant locations showed no evidence for sequential attentional sampling (Figure 6c). Yet, notably, during maintenance (Figure 6d), cross-correlations at relevant locations appeared to occur at lagged correlations, corresponding to sequential rehearsal across locations (see Figure 6a), with several non-zero time-lag cross-correlations reaching significance (i.e., $p < .05$ uncorrected, between -1300 to -1130 ms; -1000 to -800 ms; 1600 to 1700 ms; 1900 to 2000 ms). Separate cross-correlation patterns for left and right hemifield stimuli showed consistent deviations from zero, but with slightly different temporal characteristics (Landau & Fries, 2012) (Figure 6f). The temporal pattern of cross-correlations at irrelevant locations appeared more suggestive of the pattern corresponding to parallel modulation of individual locations (see Figure 6b). These results may thus suggest that during VSTM maintenance, attention sequentially focuses on memorized, relevant locations, but not on irrelevant locations. We subsequently tested the difference in temporal dynamics of attentional deployment to two stimulus or irrelevant locations within a hemifield (see Figure 7a-b), in order to compare spatiotemporal dynamics of attention to relevant and irrelevant locations. Although this analysis revealed significant differences in the temporal relationship between attention

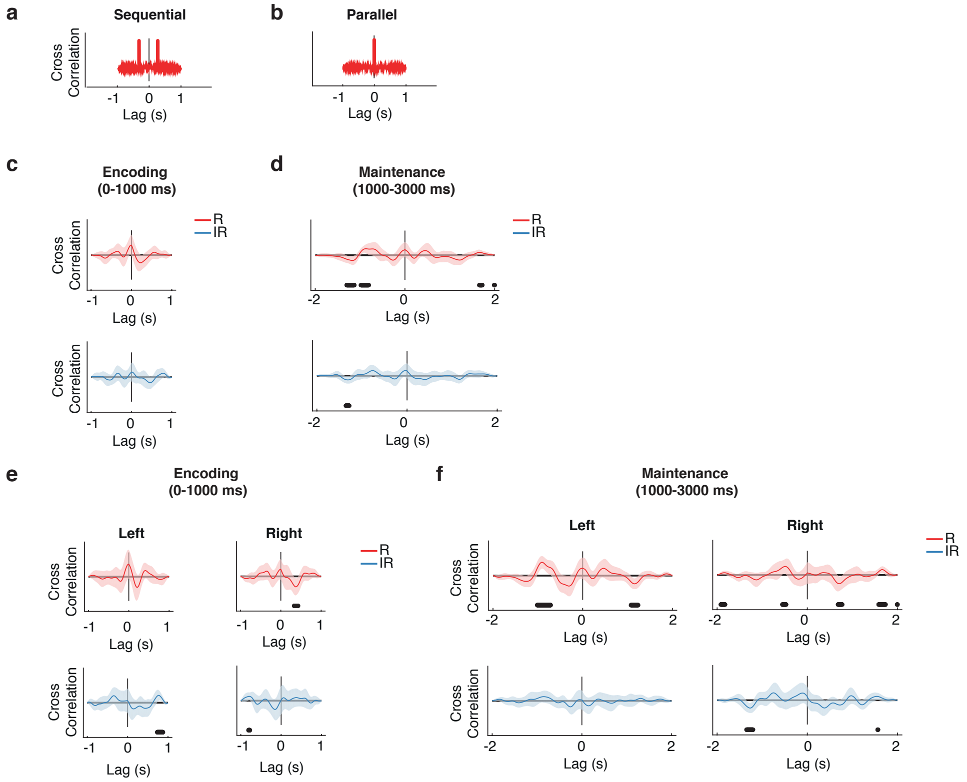

Figure 6. Cross-correlation of attentional modulation of SSVEPs at individual locations presented in the same hemifield separately for relevant and irrelevant locations. A) Hypothesized pattern of cross-correlation for sequential or rhythmic attentional modulation of two different VSTM representations. The cross-correlation deviates from 0 at lagged time points, indicative of a rhythmic relationship between attentional deployment to the two locations. B) Hypothesized pattern of cross-correlation for parallel attentional modulation of two different representations. At lag 0, the cross-correlation is high. At all other lags, the cross-correlation is close to zero, indicative of no systematic relationship between attention to these individual locations. C) Cross-correlation computed for SSVEP power modulations during VSTM encoding, using two locations presented in the same visual field, for relevant (red trace) and irrelevant (blue trace; bottom panel) locations. The confidence intervals include 0, indicating these results provide no support for sequential modulation of information of different representations. D) Cross-correlation computed for SSVEP power modulations during VSTM maintenance, using two locations presented in the same visual field, for relevant (red traces) and irrelevant (blue trace; bottom panel) locations. There appears to be sequential modulation of individual representations for relevant, but not irrelevant locations during maintenance. E) Cross-correlation computed for SSVEP power modulations during VSTM encoding, using two locations presented in left (left panel) and right (right panel) hemifield, for relevant (red traces) and irrelevant (blue trace; bottom panel) locations. As in C), these results provide no support for sequential modulation of information of different representations during encoding. F) Cross-correlation computed for SSVEP power modulations during VSTM maintenance, using two locations presented in left (left panel) and right (right panel) hemifield, for relevant (red traces) and irrelevant (blue trace; bottom panel) locations. Similar to D), cross-correlation for relevant locations reflect a pattern that supports sequential attentional modulation of individual locations during VSTM maintenance, but this pattern is not present for irrelevant locations. Black bars at the bottom of each Figure display samples for which the cross-correlation between attentional deployment to two locations reached significance.

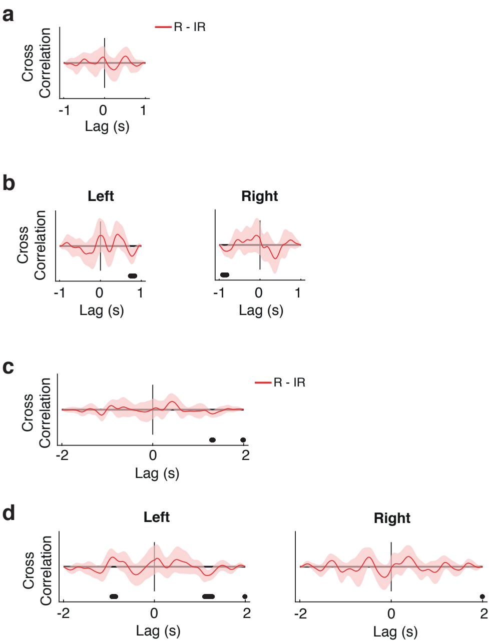

Figure 7. The difference in cross-correlation of attention to relevant versus irrelevant locations presented within one hemifield. A) When collapsing across hemifields, no differences in sequential sampling of relevant and irrelevant locations were observed during VSTM encoding. B) Analysis of the differences in cross-correlation at stimulus vs. irrelevant locations per hemifield during VSTM encoding shows differential sampling of relevant vs. irrelevant locations presented in the left, but not right visual field. C) When collapsing across hemifields, results showed no evidence for differences in sequential sampling of information presented within the same hemifield during VSTM maintenance. D) Analysis of the differences in cross-correlation at stimulus vs. irrelevant locations per hemifield during VSTM maintenance, suggests differential sampling of stimulus vs. irrelevant locations of stimuli presented in the left, but not right visual field.

to different stimulus vs. irrelevant locations, examination of these differences within each individual hemifield again revealed inconsistencies across hemifields (see Figure 7c-d). These findings provide preliminary evidence for the presence of significant lagged cross-correlations between attentional deployment to two individual stimulus locations during VSTM maintenance, in line with the idea that attention to stored representations may occur in a sequential fashion for attended, but not unattended locations (Busch & VanRullen, 2010). Yet, the current results are tenuous and should be interpreted with caution.

Discussion

The intimate relationship between selective attention and VSTM is widely acknowledged (Gazzaley, 2011; Gazzaley & Nobre, 2012; Nobre & Stokes, 2011; Shipstead et al., 2015), but our understanding of the involvement of attention during different stages of VSTM is still incomplete. In the present study, spatial and temporal characteristics of attention during VSTM encoding and maintenance were investigated under high and low memory load using SSVEPs. There were three main findings. First, we observed differences in SSVEP responses evoked at to-be-remembered vs. irrelevant spatial locations, which commenced during encoding and, importantly, continued during maintenance. This finding suggests a persistent involvement of attention throughout multiple stages of VSTM. Importantly, attentional modulations were selective to relevant locations and were absent at irrelevant locations, indicating that attention may specifically act by enhancing task-relevant sensory representations. Second, spatial attention to target locations during VSTM encoding predicted VSTM capacity across individuals, providing support for the idea that attention plays a critical role in determining the contents of VSTM. Third and lastly, exploratory cross-correlation analyses provided tentative support for sequential (rather than parallel) attentional modulation of stored representations, in line with studies showing sequential attentional sampling during perception (Fiebelkorn et al., 2013; Landau & Fries, 2012; Landau et al., 2015). Together, these findings demonstrate ongoing involvement of spatial attention during VSTM. More generally, they illustrate the usefulness of SSVEPs to continuously and simultaneously track attentional allocation to as much as six individual stimulus locations. These findings and their implications are discussed in detail below.

Attention plays a role in VSTM encoding and maintenance

Our first main finding was that attention was differentially deployed to to-be-remembered versus irrelevant locations not only during VSTM encoding, but also during VSTM maintenance. This finding corroborates and extends previous research on the role for attention during encoding of information in VSTM (Gazzaley, 2011; McNab & Klingberg, 2008). Importantly, our results show that spatial attention may not only modulate sensory activity during perceptual stages of VSTM, but also during postperceptual stages when there is no need to select sensory information for storage in VSTM and in a context of high memory load (at or above capacity). A role for spatial attention in VSTM maintenance is in line with attention-based rehearsal accounts, which posit that attention loops over stored representations stored in VSTM to keep them active (Awh et al., 2000; Awh & Jonides, 2001; Postle et al., 2004). Our results also extend findings from research demonstrating the involvement of spatial attention during postperceptual stages of VSTM using retrocues during the delay period (Griffin & Nobre, 2003; Landman, Spekreijse, & Lamme, 2003; Matsukura, Cosman, Roper, Vatterott, & Vecera, 2014; Souza & Oberauer, 2016; Sprague et al., 2016). While retrocues introduce additional attentional modulations into the task that are not necessarily inherent to VSTM, the use of SSVEPs at individual stimulus locations in this study enabled tracking of ongoing attentional allocation during VSTM maintenance without these possible confounds. This revealed an involvement of attention during VSTM, even in the absence of the need to perform attentional manipulations on stored representations.

The observed continuous attentional modulation of stimulus-specific sensory responses during VSTM is also in line with sensory recruitment theories of VSTM

(Franconeri, Alvarez, & Cavanagh, 2013; Roelfsema & de Lange, 2016; Serences, Ester, Vogel, & Awh, 2009), and previous fMRI studies showing distributed activity patterns during the delay interval reflecting feature-specific (Albers, Kok, Toni, Dijkerman, & De Lange, 2013; Emrich, Riggall, LaRocque, & Postle, 2013; Harrison & Tong, 2009), or location-specific (Sprague, Ester, & Serences, 2014; Vicente-Grabovetsky, Carlin, & Cusack, 2014) representations stored in VSTM. Additional support for the sensory recruitment hypothesis comes from studies showing that disruption of sensory activity during VSTM maintenance with transcranial magnetic stimulation (TMS) impairs VSTM performance in a topographically specific manner (Cattaneo, Vecchi, Pascual-Leone, & Silvanto, 2009; Rademaker, van de Ven, Tong, & Sack, 2016; van de Ven, Jacobs, & Sack, 2012). Importantly, VSTM-capacity is known to comprise three to four items, whereas previous studies on sensory recruitment during VSTM were typically limited to attentional tracking of one or two representations at the same time (e.g., Serences et al., 2009; Sprague et al., 2014), thus leaving unclear how attention is allocation during VSTM under a higher memory load. The present results, which indicate that VSTM may rely on continuous attentional modulations of sensory activity associated with multiple stored representations, thus extend previous findings by revealing representation-specific attentional modulations during VSTM maintenance, even when VSTM is used to its full capacity.

While VSTM maintenance has recently been posited to rely on activity-silent (hidden) distributed codes (Stokes, 2015), the present findings contradict this notion and show persistent representation-specific sensory activity during VSTM. Although our finding of persistent activity during maintenance appears in line with the abovementioned fMRI research, as well as intracranial recordings from humans and non-human primates (Supèr, Spekreijse, & Lamme, 2001; Woloszyn & Sheinberg, 2009), the observed activity patterns could alternatively reflect a hidden memory-code that becomes measurable in the neural response to the flickering placeholders (e.g., a 'ping'; Rose et al., 2016; Wolff, Jochim, Akyürek, & Stokes, 2017). Future research is needed to determine whether sensory representations during VSTM maintenance remain persistently active and are measurable even in the absence of flickering placeholders, remain active beyond the detection threshold of non-invasive techniques (Kornblith, Quian Quiroga, Koch, Fried, & Mormann, 2017), or are instead hidden unless probed by sensory stimulation (Wolff et al., 2017).

Somewhat surprisingly, the SSVEP response during encoding was weaker at relevant compared to irrelevant locations, contrary to previous findings that indicate that attention amplifies sensory processing, as reflected by stronger SSVEP responses at attended locations (Gulbinaite et al., 2014; Muller et al., 2003). This pattern reversed to the expected direction during maintenance. Two possible explanations may account for these findings. First, as the flickering placeholders directly bordered the to-be-encoded stimuli (see Figure 1a), surround suppression of the placeholders may have played a role (Fuchs, Andersen, Gruber, & Müller, 2008). Focused attention on the target stimuli presented at the center of the placeholders may have led to suppression of neuronal activity associated with processing of the surrounding placeholders, resulting in a weaker SSVEP response at relevant compared to irrelevant locations (Hopf et al., 2006). During maintenance, the focus of spatial attention may have broadened to include the placeholders themselves, resulting in stronger SSVEP responses at relevant vs. irrelevant locations. Alternatively, differences in contrast of the placeholders at relevant and irrelevant locations (i.e., placeholders contrasted with a colored stimulus vs. a white space, respectively; see Figure 1a) may have resulted in weaker figure-ground segregation at relevant compared to irrelevant locations, and thereby, a reduced SSVEP response at relevant compared to irrelevant locations (Kim & Verghese, 2012). Yet, by itself, such a low-level explanation cannot readily account for the observed flip in direction of modulations of the SSVEP response during maintenance, in which stimuli were absent at relevant as well as irrelevant locations. Moreover, the difference in SSVEP response to flickering placeholders at relevant vs. irrelevant locations during encoding predicted individual VSTM capacity across subjects, further suggesting that the observed difference in SSVP response is not simply related to differences in visual properties between relevant and irrelevant stimuli. Future research is necessary to determine to what extent surround suppression, contrast differences may have contributed to the here observed effects.

Attention to stimulus locations predicts VSTM capacity

The second main finding of this study was a relationship between VSTM capacity and the allocation of spatial attention during VSTM encoding. Low and high capacity individuals differentially allocated attention to relevant compared to irrelevant locations, in line with studies showing that individual differences in VSTM capacity are predicted by individual differences in the ability to selectively encode goal-relevant information (Fukuda & Vogel, 2009). This finding also complements previous findings showing that neural activity in subcortical and/or frontoparietal regions reflecting selective attention during VSTM predicts VSTM capacity (Liesefeld, Liesefeld, & Zimmer, 2014; McNab & Klingberg, 2008; Vogel et al., 2005), by showing that sensory activity during encoding also contributes to VSTM performance (Emrich et al., 2013; van Bergen, Ji Ma, Pratte, & Jehee, 2015). Furthermore, the functional importance of sensory activity corroborates results from a recent study showing that individual differences in the size of primary cortex predict VSTM capacity (Bergmann, Genç, Kohler, Singer, & Pearson, 2016). Like our findings, this relationship suggests that selective encoding of information in VSTM may not only depend on activity in subcortical and frontoparietal networks, but also relies on sensory activity associated with processing of stored representations.

Whereas some fMRI studies have also reported functionally relevant modulations of sensory activity during VSTM maintenance (Emrich et al., 2013; Sprague et al., 2014), deployment of spatial attention in our EEG study was selectively related to VSTM performance during encoding. FMRI is typically characterized by a much lower temporal resolution than EEG, leaving it possible that the functionally relevant attentional modulations during maintenance observed in previous fMRI research partly reflected lingering effects from the encoding interval. The lack of a similar relationship during maintenance in the present study may suggest that attentional modulation of sensory representations during maintenance is not essential for VSTM performance. Alternatively, the absence of such a relationship might be explained by a lack of substantial individual differences in the effect of attention during VSTM maintenance (Figure 5). Yet another, not mutually exclusive, explanation may be provided by our observation of sequential attentional sampling during VSTM maintenance, but not VSTM encoding. By averaging the SSVEP response across the entire maintenance interval (and hence, periods of focused attention to a given location as well as periods in which attention may have been at a different location), average SSVEP responses during maintenance may have been less reflective of strength of attentional deployment across individuals. This could perhaps also explain the absence of differential attention to the probed location on correct vs. incorrect trials during maintenance. Future research is required to determine whether attention plays a crucial role in retention of information in VSTM (Emrich et al., 2013), or whether it reflects a passive trace that is not essential for VSTM performance (Bettencourt & Xu, 2015; Vicente-Grabovetsky et al., 2014).

Use of multiple tagging frequencies to track attention to individual stimulus locations

More generally, our results show that SSVEPs provide a powerful tool to investigate the role of attention in VSTM. First, SSVEPS enable simultaneous and continuous tracking of attention to multiple items by means of stimulus-specific tags (Itthipuripat, Garcia, & Serences, 2013). This provides advantages compared to previously used electrophysiological measures used to track sensory/attentional modulations during VSTM such as gamma power modulations (Dugué, Roberts, & Carrasco, 2016; Van Vugt et al., 2014), which are difficult to link to specific memory representations, or topographical alpha power distributions (8-13 Hz), which so far have only been demonstrated during reconstruction of attention to a single location at a time (Foster et al., 2016; Samaha, Sprague, & Postle, 2016). Furthermore, the use of SSVEPs does not require interference with ongoing memory processing, which is inevitable when using retrocues to assess the role of attention during VSTM maintenance, as done in previous research (Griffin & Nobre, 2003; Kuo, Stokes, & Nobre, 2012; Souza & Oberauer, 2016). Lastly, the use of SSVEPs evoked by placeholders instead of actual stimuli enables tracking of stored representations during VSTM maintenance, during which the stimuli are physically absent. SSVEPs thus provide a valuable tool for studying the strength of sensory representations throughout different stages of VSTM. Yet, future research is necessary to determine how flickering stimuli precisely influence and interact with (top-down modulation of) induced sensory activity.

Indications of sequential sampling

Another notable finding from this study was that results from cross-correlation analyses provided more support for sequential than parallel attentional modulation of individual stimulus representations during maintenance. This pattern was not evident during encoding. Periodic reactivation of stored representations may form a plausible mechanism by which sensory activity during maintenance of information in VSTM is sustained to prevent decay (Barrouillet & Camos, 2012; Van Vugt et al., 2014), and could be the neural principle underlying attention-based rehearsal (Postle et al., 2004). Previous evidence for periodic reactivation of sensory representations came from an EEG study that showed periodic bursts in gamma power over sensory cortex during maintenance, which were interpreted to reflect periodic reactivation of stored representations (Van Vugt et al., 2014). However, periodic bursts in gamma power are difficult to map directly to specific memory representations in VSTM, and could reflect representation-unspecific increases in sensory activity. The present findings, albeit preliminary, may thus extend this previous observation and substantiate the idea that attention sequentially activates or rehearses stimulus representations during VSTM maintenance (Postle et al., 2004; Van Vugt et al., 2014).

Our observation of sequential attentional modulation of stored representations may also provide support for the influential recent proposal that the number of items that can guide attention and affect sensory processing during VSTM maintenance is limited to one, the so-called attentional template (Olivers, Peters, Houtkamp, & Roelfsema, 2011; van Moorselaar, Theeuwes, & Olivers, 2014). Possibly, individual stored items are alternately prioritized in the attentional template in a sequential fashion (Myers, Stokes, & Nobre, 2017; Olivers et al., 2011).

Surprisingly, sequential modulation of representations appeared to be specific to the maintenance interval, but was not apparent during encoding. As the encoding interval only lasted one second and the observed modulations during VSTM maintenance appeared to be fairly slow in nature, it is possible that the encoding interval was too short to detect sequential modulations of stimulus representations. Alternatively, attentional deployment to relevant locations during encoding may occur in parallel fashion for all memory items (Duncan, Ward, & Shapiro, 1994; Eimer & Grubert, 2014; Peterson et al., 2014). Of further note, during maintenance, the direct comparison of cross-correlation of attention to relevant versus irrelevant locations did not reveal significant differences, suggesting that sequential attentional modulation of relevant locations was only weakly reflected in our measures, or alternatively, that attention may have also sequentially looped across irrelevant locations to some extent. Our results should hence be interpreted with caution. Future research is necessary to replicate and extend the current findings.

Rhythmic attentional sampling during perceptual monitoring is typically observed in the alpha and/or theta range (Dugué et al., 2015; Fiebelkorn et al., 2013; VanRullen, 2016), but may slow when multiple (e.g. three) items are attended (Holcombe & Chen, 2013). This may explain why we observed relatively slow rhythmic modulations of individual representations during VSTM maintenance (i.e., ± 1/1.5 Hz). However, the current design was not optimal for determining the precise frequency of attentional modulation, due to the lack of a spatiotemporal cue that resets attention at a known time point and location (Dugué et al., 2015; Fiebelkorn et al., 2013). A closer investigation into the frequency of attentional sampling during VSTM maintenance is necessary to determine the precise temporal dynamics of attention during VSTM.

Summary

In summary, we found continuous modulations of sensory representations by spatial attention during VSTM, with modulations during encoding predicting VSTM performance. Furthermore, we report preliminary evidence for sequential attentional activation of individual stimulus representations during VSTM maintenance. More generally, our approach illustrates the usefulness of SSVEPs to simultaneously assess attentional deployment to multiple individual items during VSTM.

Acknowledgements

We thank Dr. Mike X Cohen for helpful methodological advice on the use of RESS to extract the SSVEPs from the data, and Prof. Dr. K. Richard Ridderinkhof for his guidance.

CHAPTER 4

Protecting visual short-term memory during maintenance: attentional modulation of target and distractor representations

In the presence of distraction, attentional filtering is a key predictor of efficient information storage in visual short-term memory (VSTM). Yet, the role of attention in distractor filtering, and the extent to which attentional filtering continues to protect information during post-perceptual stages of VSTM, remains largely unknown. In the current study, we investigated the role of spatial attention in distractor filtering during VSTM encoding and maintenance. Participants performed a change detection task with varying distractor load. Attentional deployment to target and distractor locations was tracked continuously by means of Steady-State Visual Evoked Potentials (SSVEPs). Analyses revealed that attention strongly modulated the amplitude of the second harmonic SSVEP response, with larger amplitudes at target compared to distractor locations. These attentional modulations commenced during encoding, and remained present during maintenance. Furthermore, the amount of attention paid to distractor locations was directly related to behavioral distractor costs: Individuals who paid more attention to target compared to distractor locations during VSTM maintenance generally suffered less from the presence of distractors. Together, these findings support an important role of spatial attention in distractor filtering at multiple stages of VSTM, and highlight the usefulness of SSVEPs in continuously tracking attention to multiple locations during VSTM.

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Introduction

Goal-directed behavior relies heavily on the ability to temporarily store goal-relevant information in visual short-term memory (VSTM). It is well known that attention plays a critical role in selective storage of goal-relevant information in VSTM, by preventing distractors from occupying the limited-capacity VSTM storage space (Awh & Vogel, 2008; Cowan & Morey, 2006; Gazzaley, 2011; McNab & Klingberg, 2008; Shipstead, Harrison, & Engle, 2015; Vogel, McCollough, & Machizawa, 2005). Selective filtering of goal-irrelevant information benefits VSTM performance by increasing the likelihood that goal-relevant information is accurately maintained in VSTM (Murray, Nobre, & Stokes, 2011). While fronto-parietal attentional networks and the basal ganglia play an important role in gating access to VSTM (Baier et al., 2010; Gillebert et al., 2012; McNab & Klingberg, 2008), it is less clear whether attentional filtering during VSTM also relies on local modulations of activity in sensory regions (Serences, 2016). Relatedly, it is still unclear to what extent attention also helps to protect VSTM content during postperceptual stages of VSTM, such as maintenance. In the present study, we addressed these questions and examined the role of attention in processing of relevant and irrelevant visuospatial information during both VSTM encoding and maintenance.

Recent studies show that attentional selection of goal relevant information does not only involve enhancement of goal-relevant sensory processing, but also entails concurrent suppression of goal-irrelevant sensory processing (Couperus & Mangun, 2010; Gaspar, Christie, Prime, Jolicœur, & McDonald, 2016; Noonan et al., 2016). Interestingly, reliance on these attentional mechanisms has been shown to vary across individuals as a function of working memory capacity (WMC). While high working memory capacity (WMC) individuals simultaneously enhance sensory processing of relevant information and suppress processing of distracting information, low WMC individuals exhibit impaired distractor suppression, and primarily enhance processing of relevant sensory information (Gaspar et al., 2016; Gulbinaite, Johnson, de Jong, Morey, & van Rijn, 2014). Studies on attentional selection in the context of VSTM have reported a similar pattern: high VSTM capacity individuals are generally more efficient at suppressing distracting information compared to low VSTM capacity individuals (McNab & Klingberg, 2008; Vogel et al., 2005). While current evidence for the role of attentional filtering during VSTM encoding is based on attentional modulation of task-irrelevant information (Fukuda & Vogel, 2009), enhancement of processing of relevant information during VSTM has received less attention. This renders it unclear if successful VSTM performance selectively relies on suppression of irrelevant sensory processing, or may also involve enhancement of goal-relevant sensory processing (Adam & Vogel, 2016;

Couperus & Mangun, 2010; Gaspar et al., 2016; Johnson & Johnson, 2009; Noonan et al., 2016).

A second outstanding question is whether attention continues to play a role in protecting the contents of VSTM after encoding, i.e., during VSTM maintenance, and if so, whether similar attentional mechanisms are at play during encoding and maintenance of information in VSTM. Existing research on the involvement of spatial attention during postperceptual stages of VSTM typically used retrocues during the VSTM delay period (Griffin & Nobre, 2003; Kuo, Stokes, & Nobre, 2012; Landman, Spekreijse, & Lamme, 2003; Matsukura, Cosman, Roper, Vatterott, & Vecera, 2014; Souza & Oberauer, 2016; Sprague, Ester, & Serences, 2016), or presented novel distractors throughout the delay interval after encoding (Bonnefond & Jensen, 2012; Rademaker, Bloem, De Weerd, & Sack, 2015). Yet, retrocues typically provide an instruction to perform additional attentional manipulations on stored representations during maintenance (Griffin & Nobre, 2003; Souza & Oberauer, 2016). Hereby, retrocues thus introduce additional attentional modulations that are not necessarily inherent to VSTM, and may interfere with ongoing maintenance of information in VSTM. Therefore, the effect of retrocues on performance and neural activity during VSTM maintenance may not necessarily generalize to regular VSTM undisturbed by an attentional cue. Although retro-cueing studies have revealed large effects of further attentional manipulations of stored representations on VSTM performance, it remains unclear to what extent attention also plays a role during typical VSTM in the absence of attentional cues or novel distractors presented during VSTM delay.

Another line of research suggesting that attention also plays a role during postperceptual stages of VSTM is based on the sensory recruitment hypothesis, which posits that attention and VSTM rely on similar neural representations that eventually serve to control motor behavior (Kiyonaga & Egner, 2013; Pasternak & Greenlee, 2005; Postle, 2015; Sreenivasan, Gratton, Vytlacil, & D'Esposito, 2014). A related hypothesis postulates that attention and VSTM share priority maps (Fecteau & Munoz, 2006; Franconeri, Alvarez, & Cavanagh, 2013; Schneider & Wascher, 2013; Serences & Yantis, 2006; Shapiro & Miller, 2011; Zelinsky & Bisley, 2015). Priority maps are modulated through selective weighting of task-(ir)relevant features represented as topographic locations in space. These modulations remain present until a particular cognitive or behavioral goal is achieved (Roelfsema & de Lange, 2016), implying that they should persist during post-perceptual stages of VSTM (Franconeri et al., 2013; Zelinsky & Bisley, 2015). In support of this hypothesis, several studies demonstrated attentional enhancement of sensory processing at stored locations during maintenance (Awh, Anllo-Vento, & Hillyard, 2000; Awh, Vogel, & Oh, 2006; Fukuda & Vogel, 2009;

Munneke, Heslenfeld, & Theeuwes, 2010; Postle, Awh, Jonides, Smith, & D'Esposito, 2004; Supèr, Spekreijse, & Lamme, 2001; Theeuwes, Kramer, & Irwin, 2011), for example during attentional refreshing of information stored in VSTM (Johnson, McCarthy, Muller, Brudner, & Johnson, 2015; Johnson, Mitchell, Raye, D'Esposito, & Johnson, 2007; Yi, Turk-Browne, Chun, & Johnson, 2008). Furthermore, fMRI studies have revealed the presence of task-relevant representations in sensory cortices during VSTM maintenance (Emrich, Riggall, LaRocque, & Postle, 2013; Pratte & Tong, 2014), where the strength of sensory activation during retention was shown to predict the quality of a memory representation (Sligte, Scholte, & Lamme, 2009). Yet, these findings were typically observed during maintenance of temporally segregated information (Emrich, Riggall, Larocque, & Postle, 2013), or were measured for a single item at a time (Fukuda & Vogel, 2009; Sligte et al., 2009). Knowledge on sensory modulations during VSTM of more cluttered displays that also contain task-irrelevant distractors is presently lacking. This leaves unclear how sensory representations contribute to VSTM in the case of more complex spatial stimulus configurations as used in typical change-detection tasks, and that better represent crowded situations in everyday life. Thus, whereas priority maps have been proposed to optimize encoding and maintenance of goal-relevant information by acting as an attentional filter (Zelinsky & Bisley, 2015), empirical evidence on their involvement in distractor suppression during VSTM is presently lacking.

In the current study, we aimed to shed more light on the role of attentional dynamics in distractor filtering during VSTM encoding and maintenance. Given that attention modulates sensory activity in a retinotopically specific fashion (Franconeri et al., 2013; Zelinsky & Bisley, 2015), we focused on the role of spatial attention in distractor filtering during VSTM. Importantly, we assessed the role of attention during VSTM without possible confounds introduced by retrocues and measured ongoing attentional modulations of multiple, simultaneously presented sensory representations of target and distractor stimuli. This way, our approach yields important insight in the role of attention for VSTM in more realistic situations in which participants need to simultaneously encode and remember multiple relevant items that first need to be selected in the presence of goal-irrelevant information. Participants performed a change-detection task in which they were asked to remember the color of three target stimuli presented among distractors and indicate if the color of a subsequent probe stimulus matched the color of the target stimulus presented at that location (Figure 1a). To investigate distractor suppression during VSTM, we varied distractor load by manipulating distractor color similarity. In the 'low distractor load' condition, all distractors had the same color, whereas in the 'high distractor load' condition, each distractor had a unique color. On half of the trials, the color of the probe was different from the color of the target at the probed location (change trials). On half of the change trials, the color of the probe stimulus was identical to the color of a stimulus at a non-probed target location ('lure trials'). Lure trials were introduced to encourage subjects to encode both the location and the color of each target stimulus.

Attentional allocation to relevant (target) and irrelevant (distractor) locations over time was measured via steady state visual evoked potentials (SSVEPs) that were elicited by placeholders at each stimulus location, as SSVEP amplitude has been shown to increase with attention (Muller, Bartelt, Donner, Villringer, & Brandt, 2003). Placeholders flickered during VSTM encoding and maintenance with unique frequency tags for relevant and irrelevant locations. Critically, this approach allowed us to continuously track attentional allocation across multiple relevant and irrelevant locations during both VSTM encoding and retention, without interfering with ongoing cognitive performance. We predicted the following patterns of results. First, at the behavioral level, we predicted that VSTM performance would be lower in the high vs. the low distractor load condition (Wolfe & Horowitz, 2004), and we predicted that the effect of distractor load would be related to individual VSTM capacity (Awh & Vogel, 2008). Second, at the neural level, we predicted to find distractor suppression, reflected in reduced SSVEP responses at distractor compared to target locations during both VSTM encoding and maintenance, in particular on high compared to low distractor load trials. Third, we expected that the amount of attention paid to the distractors would have a direct effect on behavioral performance, such that individuals exhibiting stronger suppression of distractor representations during VSTM would show a reduced effect of distractor load on VSTM performance.

Results

Forty-four participants completed the experiment. One participant was excluded because of chance-level performance on the change detection task, and another participant was excluded because of technical issues during EEG data collection. Three participants were excluded from further analyses because they made eye movements towards the flickering placeholders on more than 30% of the trials, and two were excluded because their EEG data was severely contaminated by blink and/or muscle artifacts. Our final sample for behavioral analysis consisted of 37 participants (M = 21.8 years; 26 F). The average partial symmetry span score on the complex working memory task was 30.5 across participants (SD 7.31; range 12-42). Two additional participants showed no SSVEP in the raw EEG data (power at the flicker frequencies was indistinguishable from power at neighboring frequencies; determined based on

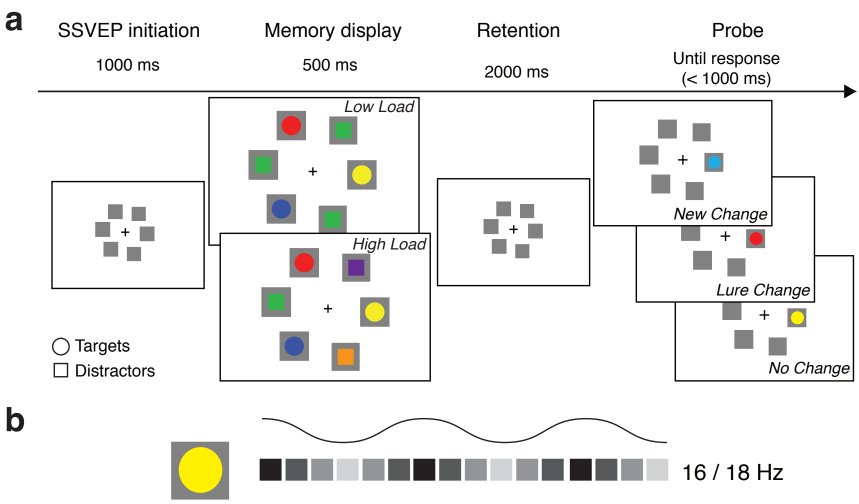

Figure 1. Experimental design. a) Graphical display of the change-detection task with distractors. In this example targets were circles, and distractors were squares. In each trial, participants were shown a memory display with homogenously (low distractor load; top panel) or heterogeneously colored distractors (high distractor load; bottom panel). Distractor load was manipulated block-wise. After a retention interval, a probe stimulus was presented at one of the target locations. The probe could either have a new color (new change trials; top panel), a color of one of the target stimuli at a non-probed location (lure trials; middle panel), or a color identical to the target stimulus at that location (no change; bottom panel). b) Stimulus contrast of the placeholders at stimulus locations was manipulated in a sinusoidal fashion from black to white to elicit SSVEPs at 16 and 18 Hz. Target and distractor locations flickered at different frequencies.

visual inspection of frequency spectrum of the sixteen most posterior channels; see the Methods section for details) and were excluded from further SSVEP analyses. Our final sample for SSVEP analyses thus consisted of 35 participants (M = 21.6 years; 26 F).

The effect of distractor load on VSTM performance

To examine our first prediction that VSTM performance would be lower in the high vs. the low distractor load condition, we conducted a repeated measures ANOVA with distractor load (low; high) and trial type (no change; new change; lure change) as within-subject factors. This analysis revealed no main effect of distractor load on accuracy of performance ($F_{1,36} = 1.851$, $p = .182$, see figure 2a), but instead showed a significant interaction between distractor load and trial type ($F_{1.9,67.5} = 3.868$, $p = .025$). This interaction was due to a selective effect of distractor load on performance on no-change trials: Post-hoc comparisons revealed that accuracy on no-change trials was lower for the high (M = 65%) compared to low distractor load condition (M = 69%; $t_{36} = -2.456$, $p = .02$; see Figure 2b), whereas the effect of distractor load was not significant on new change and lure change trials (all p's > .37). Notably, we also observed a main effect of trial type ($F_{1.5,54.1} = 41.233$, $p < .001$), reflecting much poorer performance on no-change (M = 67%) compared to new change (M = 91 %; $t_{36} = -9.081$, $p < .001$) and lure change trials (M = 79%; $t_{36} = -4.453$, $p < .001$). Further, planned comparisons showed that performance was worse on lure (M = 79%) compared to new change trials (M = 91 %; $t_{36} = -4.627$, $p < .001$). Analyses of participants' sensitivity to detect a change under different distractor loads (low; high) across trial types (new change; lure change) using d' (Macmillan & Creelman, 2004) yielded similar results (main effect of trial type; $F_{1,36} = 13.377$, $p < .001$, with poorer performance on lure change trials). As perfect binding of color to location would have resulted in equal performance on new change and lure change trials, this indicates that participants did not always perfectly bind stimulus color to location. Thus, distractor load only affected performance accuracy in no-change trials, the trial type on which accuracy of performance was the lowest.

Reaction time analyses also revealed a main effect of trial type ($F_{1.9,68.6} = 38.331$, $p <$ .001, see Figure 2d), but no main effect or interactions with distractor load (see Figure

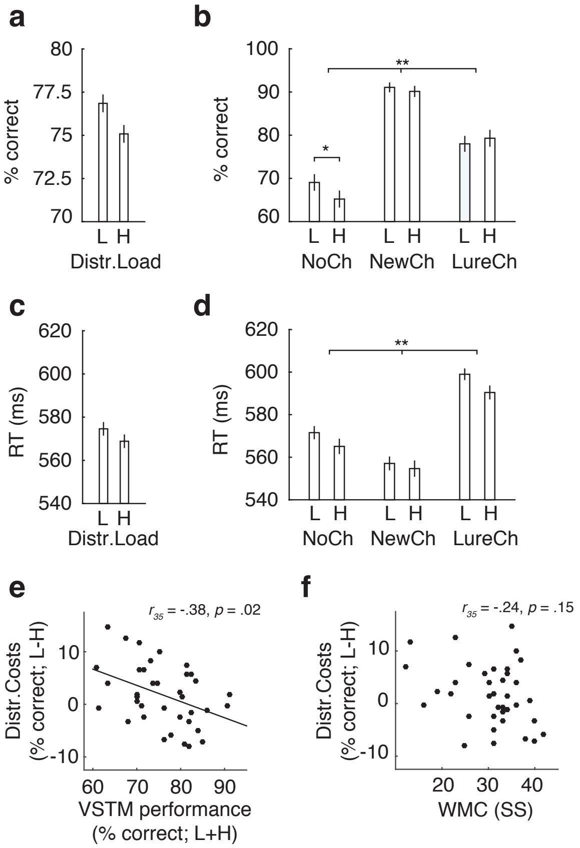

Figure 2. Behavioral performance on the change-detection task. A) Accuracy of performance shown separately for low and high distractor load trials (averaged across trial type). B) Accuracy of performance shown separately per trial type (no change; new change; lure change) and condition (low vs. high distractor load). Performance accuracy was lowest on no-change trials. Only in these trials, impaired performance was observed in high compared to low distractor load trials. C) Response times on the task shown separately for low and high distractor load trials (averaged across trial type). D) Response times per trial type (no change; new change; lure change) and condition (low vs. high distractor load). Response times differed across trial types, but were not affected by distractor load. E) VSTM capacity (average performance on low and high distractor load trials) negatively predicted the effect of distractor load on VSTM performance (performance on high minus low distractor load trials), such that a high distractor load generally impaired performance more in low vs. high capacity individuals. F) WMC as measured on the symmetry span task was not significantly related to the effect of distractors on performance. Error bars represent the standard error of the mean.

2c). Post-hoc t-tests showed that participants were slower to respond on no-change compared to change trials ($t_{36} = 2.747$, $p = .020$), as well as lure change trials ($t_{36} = -5.826$, $p < .001$). Planned contrasts showed that participants were also slower on lure change compared to new change trials ($t_{36} = -8.573$, $p < .001$), indicative of imperfect binding of color to location. The effect of distractor load on performance was thus selective to accuracy of performance on the relatively difficult no-change trials.

Individual differences in the effect of distractor load on accuracy of performance

Based on previous research on individual differences in the effect of distractors on performance as a function of VSTM capacity (Vogel et al., 2005), we also predicted that sensitivity to distraction would vary as a function of individual VSTM capacity. To test this prediction, we examined if VSTM capacity measured on the change detection task, and WMC as measured on a symmetry span task (administered in a separate session), predicted the effect of distractor load on accuracy of performance (distractor costs; % correct on low minus high distractor load trials). This analysis showed a negative correlation between VSTM capacity and behavioral distractor costs ($r_{35} = -.380$, $p = .020$; Figure 2e), in line with our prediction and previous research showing that individuals with a high VSTM capacity are better at filtering out distractors (Fukuda & Vogel, 2009; Vogel et al., 2005) (repeating this analysis post-hoc including the no-change trials only yielded a similar result: $r_{35} = -.501$, $p = .002$). As can also be seen in Figure 2e, low capacity individuals showed a stronger impairment in the high distractor load condition, whereas high capacity individuals showed poorer performance in the low distractor load condition (reflected in negative distractor costs). The correlation between the effect of distractor load on VSTM performance and WMC measured on the symmetry span task was in the same direction, albeit not significant ($r_{35} = -.242$, $p = .148$; see Figure 2f; repeating this analysis post-hoc using only the no-change trials did reveal a significant relationship between WMC and distractor costs; $r_{35} = -.331$, $p = .047$).

SSVEP results: modulation by spatial attention

The interval- and condition-average frequency spectrum and topographical distribution of the SSVEPs at the flicker frequencies is displayed in Figure 3a. Attentional deployment to target vs. distractor locations under different distractor loads was assessed using a repeated measures ANOVA with location (target; distractor), distractor load (low; high) and interval (encoding; maintenance) as within-subject factors. In contrast to our second prediction, no difference in SSVEP response at the flicker frequencies was observed at target compared to distractor locations ($F_{1,34} = 3.40$, $p = .074$). If anything, SSVEP amplitude was numerically higher at distractor locations (see Figure 3b). Other main effects or interactions were also not significant (all *p*'s > .10). Thus, these results provide no support for modulation of attention to target and distractor locations during VSTM encoding or maintenance, or an effect of distractor load on the distribution of spatial attention.

Given that previous research has shown that attentional modulations of SSVEP amplitude may be restricted to the second harmonic of the SSVEP (Kim, Grabowecky, Paller, & Suzuki, 2011), we next examined the presence of attentional modulations at target and distractors locations using the second harmonic of the SSVEP. The interval- and condition-average frequency spectrum and topography of the second harmonic of the SSVEP are displayed in Figure 4a. A repeated measures ANOVA revealed a significant main effect of location ($F_{1,35}$ = 7.318, *p* = .011). Follow-up comparisons revealed an increased SSVEP response at target compared to distractor locations during encoding (t_{34} = 2.224, *p* = .040), as well as maintenance (t_{34} = 3.320, *p* = .011; see Figure 4b). No other main effects or interactions were significant, suggesting that at the group level, distractor load did not differentially affect attentional allocation to target or distractor locations during VSTM encoding and/or maintenance. In short, spatial attention continuously modulated target and distractor representations during VSTM independently of distractor load, and this was selectively captured in the second harmonic of the SSVEPs.

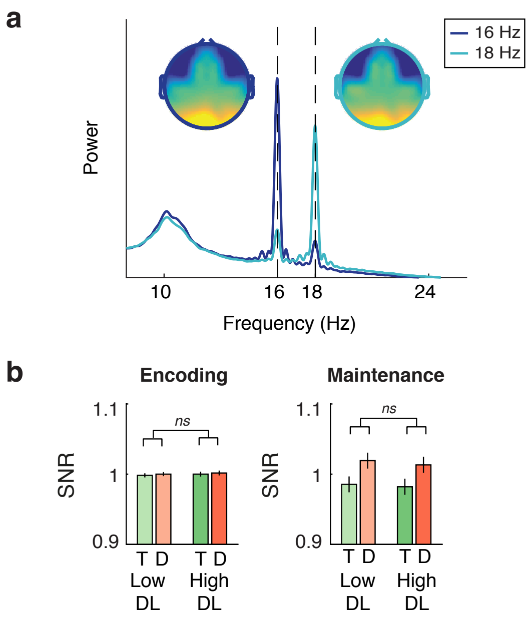

Figure 3. SSVEP responses at the fundamental frequency. a) Frequency spectrum and topography of the RESS time series optimized for 16 (dark blue) and 18 Hz (light blue) activity, computed using the condition-average data in the time-window during which the flickering placeholders were on screen and the SSVEP was stable (-500 to 2500 ms; the y-axis reflects arbitrary power units as the RESS time series were computed based on multivariate source separation). At the group level, topographies show strong overlap between frequencies. The frequency spectra confirm distinct differences between the group average RESS time series for 16 and 18 Hz in terms of their frequency content. b) SSVEP response (computed as the normalized SNR) for target (T; green) and distractor (D; red) locations, showing no significant differences in SSVEP power between target and distractor locations. Distractor load (DL; low vs. high; light vs. dark shades respectively) also did not affect SSVEP power. Error bars represent the standard error of the mean.

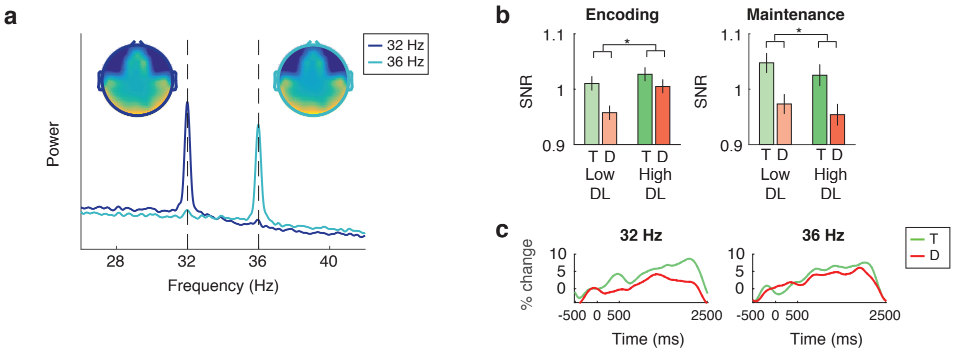

Figure 4. SSVEP responses at the second harmonic. a) Frequency spectrum and topography of the RESS time series optimized for the second harmonics of the SSVEP at 32 (dark blue) and 36 (light blue) Hz, computed using the condition-average data in the time-window during which the flickering placeholders were on screen and the SSVEP was stable (-500 to 2500 ms), using the condition-average data (the y-axis reflects arbitrary power units as the RESS time series were computed based on multivariate source separation). The average topographies of the two frequencies show strong overlap, but differ from the topographies of the SSVEP at the fundamental frequency (see Figure 3a). The frequency spectra show distinct differences between the two RESS time series in terms of their frequency content. b) SSVEP response (computed as the normalized SNR) for target (T; green) and distractor (D; red) locations. SSVEP responses were stronger at target compared to distractor locations during both VSTM encoding and maintenance. Distractor load (DL; low vs. high; light vs. dark shades respectively) did not affect SSVEP power. c) Time course of the SSVEP, displayed as the % change in activity relative to the baseline (-200 to 0 ms), for the target (green) and distractor (red) locations at 16 Hz (left panel), and 18 Hz (right panel). The time course was obtained via the Hilbert transform of the bandpass filtered RESS time series (FWHM 3 Hz) for each frequency and condition (targets and distractor locations). Prior to baseline normalization, for each time point, the bandpass-filtered and Hilbertized power at the neighboring frequencies (spaced ± 2, 2.5, 3 Hz distance) was subtracted from the power at the frequencies of interest (similar to the computation of the SSVEP response shown in b). Error bars represent the standard error of the mean.

Individual differences in distractor processing during VSTM

In line with previous findings (Luck & Vogel, 2013; Vogel et al., 2005) and our first prediction, analysis of the behavioral data showed that individual short-term memory capacity was significantly related to sensitivity to distractors. We therefore also assessed whether the attentional modulations observed in the second harmonic of the SSVEP were related to individual differences in the effect of distractor load on behavior. To this end, we included distractor costs as a covariate in the repeated measures ANOVA in which we tested the effect of location (target; distractor) and distractor load (low; high) on amplitude of the second harmonic of the SSVEP (note that we collapsed across time intervals since these showed no effect in the ANOVA, see previous section). Inclusion of behavioral distractor costs revealed a significant three-way interaction between location, condition, and distractor costs ($F_{1,33} = 5.384$, $p = .027$), suggesting that the way in which distractor load affected attentional deployment to target vs. distractor locations predicted behavioral distractor costs.

To visualize the observed interaction, we defined two groups of participants based on a median split of distractor costs: Individuals who, on average, showed larger distractor costs in the low distractor load condition (group 1), and individuals who, on average, showed larger distractors costs in the high distractor load condition (group 2; see Figure 5a). This median split illustrates that modulations of spatial attention were only visible in the distractor load condition in which participants performed best, but were not apparent in the condition in which performance was more severely impaired by distractors. This was confirmed by a post-hoc correlation test in which we correlated the behavioral effect of distractor load to the effect of distractor load on the difference in attentional allocation to target vs. distractor locations (r_{33} = -.41; *p* = .01; see Figure 5b). Although our analysis did not reveal a significant interaction with the effect of time (encoding vs. maintenance), we post-hoc assessed whether the relationship between the effect of distractor load on differential modulation of target and distractor locations

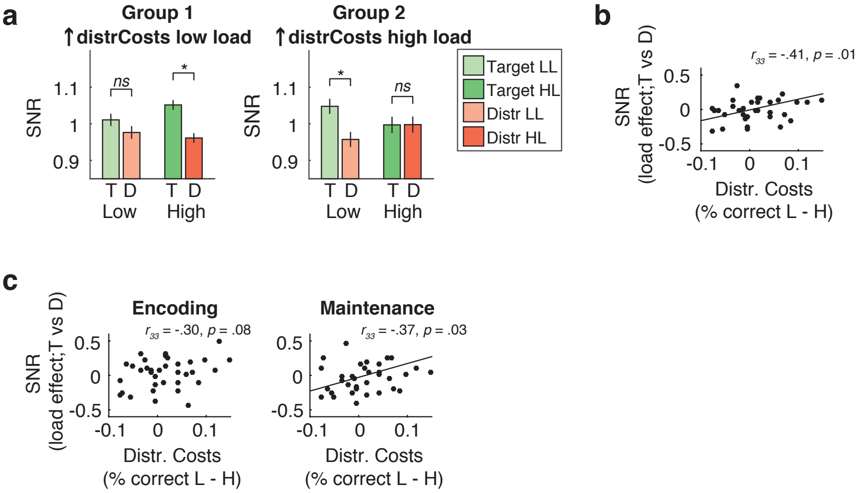

Figure 5. Individual differences in attentional modulation of the second harmonic SSVEP relate to VSTM performance. a) Graphical display of the three-way interaction between the effect of location (T vs. D), condition (low vs. high), and behavioral distractor costs, by means of a median split of participants based on distractor costs. Group 1 consists of participants with low distractor costs (group-average distractor costs were negative in this subgroup), who performed better in the high compared to the low distractor load condition. Participants in group 2 showed high (positive) distractor costs, and thus performed better in the low compared to high distractor load condition. Within each subgroup, differential allocation of attention across target and distractor locations was apparent in the condition in which participants performed best, but was not observable in the condition in which they failed to prevent distractors from interfering with VTSM performance. A post-hoc significant negative correlation between behavioral distractor costs and the difference in attentional allocation to target vs. distractor locations in the high vs. low distractor load condition (double subtraction) confirmed the interaction observed in the ANOVA, b) averaged across VSTM encoding and maintenance, and c) separately for the encoding and maintenance interval. Individuals who paid more attention to target vs. distractor locations under high distractor loads generally displayed reduced VTSM impairments in the high compared to the low distractor load condition. Error bars represent the standard error of the mean.

during VSTM was present during encoding and maintenance alone, as this could strengthen support for the notion that attention filtering during VSTM maintenance contributes to performance. Results showed that the cross-subject relationship between the effect of distractor load on VSTM performance and on attention to target and distractor locations, was at trend level during VSTM encoding (r = -.30, *p* = .08), and reached significance during VSTM maintenance (r = -.37, *p* = .03; see Figure 5c). This suggests that differential attentional deployment across target and distractor locations helps to protect the stored contents of VSTM during VSTM maintenance.

To determine if the observed relationship between the effect of distractor load on performance and attentional allocation to target vs. distractor locations was driven by changes in attention to target locations, changes in attention to distractor locations, or both, we post hoc separately correlated the difference in the SSVEP amplitude in the high vs. low load condition at target (or distractor) locations with the effect of distractors on behavior. This revealed no evidence for a selective relationship between the effect of distractor load on target amplitude or distractor amplitudes (all *p*'s < .25), suggesting that individual differences in how distractor load affected performance did not selectively reflect individual differences in distractor suppression or target enhancement (Gaspar et al., 2016). Instead, individual differences in the effect of distractor load on the ***relative*** distribution of attention to target versus distractor locations predicted the effect of distractors on individual performance.

Discussion

Previous research has shown that attention plays a critical role in encoding goal-relevant information in VSTM by preventing interference from distracting information. In the current study, we examined the distribution of spatial attention (as measured by SSVEP amplitude) across task-relevant and task-irrelevant locations during both encoding and maintenance stages of VSTM under conditions of high and low distractor load. We report three main findings. First, in line with previous research (Cowan & Morey, 2006; Fukuda & Vogel, 2009), we found that individual differences in the effect of distractor load on behavior were related to VSTM capacity, such that low-capacity individuals suffered more when distractor load was high compared to high-capacity individuals. Second, we found that attention strongly modulated the amplitude of the second harmonic SSVEP response, with larger amplitudes at target compared to distractor locations during VSTM maintenance. Lastly, cross-subject analyses revealed a relationship between the deployment of spatial attention to target vs. distractor locations and the effect of distractor load on behavioral performance. Specifically, individuals who showed stronger differentiation of attention to target versus distractor locations, showed less distractor-related performance impairments. Together, these findings indicate that spatial attention not only determines the quality of sensory representations during VSTM encoding, but may also help to preserve sensory representations during VSTM maintenance.

Extending previous studies demonstrating the importance of attention during VSTM encoding in the presence of distraction (Cowan & Morey, 2006; Fukuda & Vogel, 2009; Gazzaley, 2011; Vogel et al., 2005), we observed differential attentional deployment across target and distractor locations that commenced during VSTM encoding, and importantly, persisted during VSTM maintenance. This finding may suggest that selective attention not only supports VSTM during encoding, but also plays an important role in preserving VSTM contents during VSTM maintenance. Moreover, it corroborates previous findings showing that attention can filter irrelevant perceptual information by modulating sensory activity (Gazzaley, 2011; Gulbinaite et al., 2014; Murray et al., 2011), and reveals that such sensory modulations persist during post-perceptual stages of VSTM, i.e., during maintenance of stored information. This may suggest that retention of information and attending to information rely on shared neural populations or mechanisms in sensory regions (Kiyonaga & Egner, 2013; Pasternak & Greenlee, 2005; Shapiro & Miller, 2011; Zelinsky & Bisley, 2015), in line with the sensory recruitment account of VSTM (Serences, 2016).

Thus far, the role of attention during VSTM maintenance has mostly been examined by presenting distractors during the delay interval, i.e. after target encoding (Bonnefond & Jensen, 2012; Hönegger et al., 2011; Rademaker et al., 2015; Sreenivasan & Jha, 2007), or by presenting retrocues or instructions to refresh certain stored representations during the maintenance interval (Griffin & Nobre, 2003; Johnson et al., 2007; Kuo, Stokes, & Nobre, 2012; Murray et al., 2011). Our findings indicate the involvement of attentional modulations during typical maintenance of information in VSTM regardless of the need to suppress new perceptual input during the VSTM delay interval. This is important as findings from a recent behavioral study revealed that filtering of distractors presented along goal-relevant information during VSTM encoding is unrelated to filtering of newly presented distractors during the VSTM delay period (McNab & Dolan, 2014), suggesting these processes may rely on different neural mechanisms. Furthermore, our results reveal that attention plays an essential role in accurate maintenance of representations in VSTM, even when there is no need for further attentional selection of stored representations during maintenance (e.g., following retrocues (Griffin & Nobre, 2003; Kuo, Stokes, & Nobre, 2012)). By probing attentional modulations of target and distractor locations throughout VSTM without introducing novel task-irrelevant distractors or retrocues during the delay interval, we were able to demonstrate that attentional deployment also supports typical VSTM maintenance. Future research is necessary to determine whether attentional filtering of distraction during the encoding interval and attentional filtering of distraction presented during maintenance indeed rely on different neural mechanisms.

Another main finding of the current study was that the extent to which an individual allocated attention to target relative to distractor locations during VSTM predicted the extent to which distracting information impaired VSTM performance. Specifically, we found that individuals who paid more attention to target versus distractor locations generally showed less distractor-related interference of VSTM performance than individuals who did not. These results may suggest that attentional modulations of sensory activity form a powerful mechanism that helps to preserve information in VSTM even when distraction is no longer physically present. Taking the differential allocation of spatial attention across target and distractor locations to reflect an attentional filter (Zelinsky & Bisley, 2015), this finding extends previous observations that individual differences in distractor filtering during encoding predict distractor-related impairments in VSTM performance (McNab & Klingberg, 2008; Vogel et al., 2005).

In line with our findings, a recent ERP study reported impaired filtering abilities in low-capacity individuals, that were, importantly, accompanied by larger sensory responses to probe stimuli at distractor locations immediately following VSTM encoding in low-capacity, relative to high-capacity individuals (Fukuda & Vogel, 2009). Based on these results, the authors suggested that the impaired filtering ability in low-capacity individuals arises from the inability to recover from momentary attentional capture by task-irrelevant distractors (Fukuda & Vogel, 2009; Keisuke Fukuda & Vogel, 2011). Our findings suggest that distracting information may continue to affect attentional allocation to target vs. distractor locations long after this information has disappeared, throughout VSTM maintenance, and that individual differences in ongoing, not just momentary, attentional allocation to relevant and irrelevant locations predict filtering ability during VSTM.

Importantly, across individuals, relative attentional deployment to target vs. distractor locations predicted the effect of distractors on VSTM performance, but attention to target or distractor locations alone did not. Although this result corroborates previous findings showing the close interplay between relative enhancement vs. suppression of goal-(ir)relevant information during attentional selection (Couperus & Mangun, 2010), we did not find evidence for a selective failure to suppress distraction in low-capacity individuals (Fukuda & Vogel, 2009; Gaspar et al., 2016). Thus, relative differences between target enhancement and distractor suppression may be a better predictor of VSTM performance accuracy than suppression of distractors alone.

Notably, distractor load exerted different effects on VSTM performance in low- and high-capacity individuals. At the group level, we observed the expected pattern of increased distractor-related performance impairments for high compared to low distractor loads, although this effect was selective to no-change trials (Andersen, Muller, & Hillyard, 2015). However, the effects of distractor load on VSTM performance varied in direction in a systematic fashion based on VSTM capacity: Low-capacity individuals performed worse in the high compared to low distractor load condition, whereas the opposite was true for high-capacity individuals, who performed best under high distractor loads. It is conceivable that low- and high-capacity individuals may have used different strategies to filter distraction, resulting in different effects of distractor load on performance (Vicente-Grabovetsky, Carlin, & Cusack, 2014). Yet, our observation that optimal task performance was accompanied by increased attention to target vs. distractor locations across all participants, speaks against this scenario. An alternative explanation could be that the effect of memory load and distractor load interacted. This would be in line with the proposal that the ability to focus attention improves under task conditions of high perceptual load, but deteriorates under conditions of high cognitive load (e.g., when working memory is loaded) (Lavie, 2010). According to this account, when cognitive load is low (e.g., for high VSTM capacity individuals), a high perceptual load (high distractor load condition) leads to more successful filtering. When cognitive load is high on the other hand (e.g., for low-capacity individuals), this results in an overall impairment of filtering ability, leading to poorer performance under high compared to low distraction conditions. In other words, when taking VSTM capacity as an inverse proxy of cognitive load (low-capacity individuals will have experienced a higher cognitive load), and distractor load as the perceptual load induced by the task, our pattern of findings is in line with the idea that cognitive load and perceptual load interact to affect the ability to filter distractors (Lavie, 2010; Shimi, Woolrich, Mantini, & Astle, 2014).

An important, but unanticipated finding was that the observed attentional modulations were selective to the second harmonic of the SSVEP response. We had also expected to find effects of attention on the fundamental frequency component of the SSVEP (Gulbinaite et al., 2014; Muller et al., 2003). It is possible that we did not observe effects of our attentional manipulation on the fundamental SSVEP response because the SSVEPs were generated by flickering placeholders around the stimulus locations (see Figure 1a) instead of flickering stimuli presented at the stimulus locations themselves. This may have resulted in surround suppression of the placeholder (surrounding the stimulus location), thereby also suppressing the fundamental frequency response of the SSVEP (Fuchs, Andersen, Gruber, & Müller, 2008; Hopf et al., 2006). Given that surround suppression was likely stronger for attended compared to irrelevant locations (Hopf et al., 2006), this could also explain why we observed a trend for a reduced (rather than enhanced) fundamental SSVEP response at target compared to distractor locations (see Figure 2b).

Yet, we are not the first to report the selective presence of attentional modulations in the second harmonic instead of the fundamental frequency of the SSVEP (Kim et al., 2011; Pei, Pettet, & Norcia, 2002; Peterson et al., 2014). An alternative explanation for why the second harmonic SSVEP response was more sensitive to attention in our and other studies is that fundamental and harmonic SSVEP responses may be generated by different neural populations and/or brain regions that may respond differently to particular stimulus properties and/or attentional manipulations. For instance, the fundamental frequency response may be primarily generated in striate cortex, whereas the harmonics of the SSVEP may be generated in extrastriate regions or more dorsal and anterior regions (Kim et al., 2011; Pastor, Valencia, Artieda, Alegre, & Masdeu, 2007). The different topographical and functional characteristics of the fundamental and harmonic frequency components of the SSVEP have been speculated to reside in differential involvement of subcortical (fundamental) versus cortico-cortical (harmonic) communication (Pastor et al., 2007), or in increased top-down control over generators of the harmonic compared to the fundamental SSVEP component (Kim et al., 2011; Pastor et al., 2007). Yet, actual knowledge on the neuroanatomical basis of the fundamental and harmonic frequency components of the SSVEP is presently remarkably limited (Kim et al., 2011; Norcia, Appelbaum, Ales, Cottereau, & Rossion, 2015; Pastor et al., 2007). Future research is necessary to determine the influence of various bottom-up and top-down effects on the fundamental frequency and second harmonic of the SSVEP and to increase understanding of the functional differences between these responses (Kim et al., 2011), for instance through systematic comparisons of the effect of bottom-up (e.g., surround-suppression; Reynolds & Heeger, 2009) and top-down factors (e.g., attention) on the same frequency SSVEP as a fundamental or harmonic response to a flickering stimulus (Pastor et al., 2007). This will not only help to form more accurate hypotheses in experiment design, but will also provide important insights into properties of the visual system related to bottom-up and top-down modulations of visual processing.

The use of SSVEPs in the current study enabled us to continuously track attention to target and distractor locations during VSTM. Yet, the current design does not permit investigation of the temporal dynamics of attentional allocation to each individual target and distractor location. Contradictory to the conception of a multifocal and tonically divided attentional focus (Muller et al., 2003), recent studies indicate that attention may rhythmically sample across locations and objects (Fiebelkorn, Saalmann, & Kastner, 2013; Landau & Fries, 2012). Potentially, our finding of prolonged and continuous differential attentional deployment to target and distractor locations during VSTM is a result of averaged rhythmic modulations of SSVEP amplitude across locations and trials (Stokes & Spaak, 2016). As we tagged all target and all distractor locations with the same frequency on every trial, we were not able to disentangle attentional allocation to individual stimulus locations using the present task design. The temporal dynamics of the deployment of attention during VSTM is an interesting and important venue for future research. Moreover, previous studies on attentional filtering in service of VSTM have indicated an important role for frontal regions and the basal ganglia in preventing distractors from interfering with VSTM (Baier et al., 2010; McNab & Klingberg, 2008). An interesting question for future research concerns the involvement of these regions in modulating sensory representations to filter distracting information during VSTM retention. Lastly, additional studies are necessary to further examine the functional relevance of the distractor-related attentional modulations observed in the current study (Roelfsema & de Lange, 2016). Based on the observed correlation between distractor costs and attentional deployment during VSTM, we cannot infer whether the allocation of attention is functional and serves storage of information in VSTM (Awh, Jonides, & Reuter-Lorenz, 1998; Postle et al., 2004), or alternatively, whether attentional allocation is driven by VSTM contents but is not necessary for accurate performance (Belopolsky & Theeuwes, 2009; Clark, Noudoost, & Moore, 2012). Studies in which the behavioral consequences of disrupting retinotopic modulation of spatial attention during VSTM maintenance are investigated (Eštočinová, Gerfo, Della Libera, Chelazzi, & Santandrea, 2016), will be informative in this respect.

To summarize, in this study, we show distractor-related modulations of spatial attention during VSTM that last during VSTM maintenance and predict effects of distraction on VSTM performance. Attention may thus help to protect the contents of VSTM during post-perceptual stages of VSTM.

Methods

Participants

Forty-four participants were recruited using the online participant recruitment system of the Psychology Department of the University of Amsterdam and participated in return for monetary compensation or course credits. Participants were neuropsychologically healthy (assessed based on self-report), and were screened for color-blindness, right-handedness, epilepsy and migraine. Informed consent was obtained from all participants before the start of the experiment. The procedure for the experiment was approved by the local ethics committee of the University of Amsterdam, and was in accordance with the approved guidelines and regulations. As detailed in the results section, our final sample consisted of 37 participants (M = 21.8 years; 26 F).

Experimental task

Participants performed a VSTM change detection task (partially modeled after; Mall, Morey, Wolff, & Lehnert, 2014) in which they had to remember the color and location of three targets that were presented in the presence of three distractors (see Figure 1a). The total number of stimuli (six) exceeded average VSTM capacity (Luck & Vogel, 2013), necessitating filtering of distractors for accurate storage of the targets (Fukuda & Vogel, 2009). Stimulus presentation and response registration were controlled using Psychtoolbox (Brainard, 1997) and Matlab (The MathWorks). Stimuli were displayed on a 24-inch monitor with a 144 Hz refresh rate. Target and distractor stimuli had different shapes (squares/circles; .9/1.02 degrees visual angle (dva) diameter), and the assignment of shape (squares/circles) to stimulus type (targets/distractors) was counterbalanced across participants. All stimuli had clearly distinct, but equiluminant colors (difference between colors < 10 cd/m2). Stimuli were presented on square placeholders (width/height 1.2 dva), positioned on a ring around fixation (placed at 4 dva from fixation). Placement of stimuli across locations occurred in a pseudorandom fashion such that target stimuli were always placed across both hemifields. Participants thus had no predictive information regarding the location of the targets and distractors preceding presentation of the memory display, and needed to reactively select the targets from distractors based on stimulus shape. Distractor load was manipulated through distractor color similarity. In the 'low distractor load' condition, all distractors had the same color, whereas in the 'high distractor load' condition, each distractor had a unique color (see Figure 1a).

In order to track attentional allocation across space and time, we used frequency tagging of stimulus locations to evoke SSVEPs separately for target and distractor locations (Gulbinaite et al., 2014). Hereto, stimulus placeholders changed luminance from black to white in a sinusoidal fashion (see Figure 1b). The flicker frequency assigned to each placeholder in a given trial was based on the stimulus type presented at the placeholder (target vs. distractor), such that target and distractor locations were each tagged with a unique flicker frequency. The tagging frequencies used were spaced closely together in the frequency spectrum (16 and 18 Hz) to minimize perceptual differences between the placeholders that could affect attentional deployment, and were outside the frequency range of endogenous oscillatory activity usually observed during VSTM, such as theta and alpha activity (Klimesch, 1999; Roux & Uhlhaas, 2014; Vissers, van Driel, & Slagter, 2016). The assignment of frequencies to target vs. distractor locations was counterbalanced across conditions (low vs. high distractor load). Prior to the start of the experiment, participants received instructions about the shape of targets and distractors (the assignment of stimulus type to shape was constant throughout the experiment for each participant), and were explicitly informed that distractor colors were irrelevant for accurate performance on the task. Participants received no information about the distractor manipulation between conditions.

Each trial started with a 1000 ms presentation of six flickering placeholders in order to obtain a stable SSVEP response to the flickering placeholders. Subsequently, a memory array with distractors was presented within the placeholders for 500 ms, which was followed by maintenance interval of 2000 ms during which the stimuli were removed from the screen but the flickering placeholders remained present. Placeholders flickered throughout the entire trial until presentation of the probe. The probe stimulus was presented on a placeholder at a randomly selected target position, and its color was different from the color of the probed target in the memory display on half of the trials (change trials).

To ensure that participants bound stimulus colors to stimulus locations, we manipulated the color of the probe stimulus such that on half of the change trials the probe color was identical to the color of a stimulus at a non-probed target location (‘lure trials’). On the other half of change trials, the probe would adopt a ‘new’ color (‘new change trials’; see Figure 1a). Binding of stimulus color to location would result in an equal performance on lure and new change trials, whereas a lack of color-location binding (e.g., if participants would simply verbalize target colors) should result in impaired performance on lure trials. This manipulation thus enabled the assessment of the degree to which participants bound stimulus color to location during VSTM. Lure and new change trials were randomly interspersed among no-change trials.

On presentation of the probe, participants indicated whether the color of the probe was identical to the color of the target at the probed location by pressing one of two response buttons placed on the right armrest of the chair (right index finger for no change; right middle finger for change). After a response was made or when the response interval (1000 ms) elapsed, the placeholders were removed from the screen. An inter trial interval (ITI) of 1000 ms preceded the next trial. A central fixation-cross was shown during the entire trial. Participants were instructed to keep their eyes at fixation at all times.

The experiment consisted of 6 blocks of 64 trials. Distractor load was manipulated block-wise, and the condition (low vs. high distractor load) with which the experiment started was counterbalanced across participants. Participants were allowed a self-paced break after every 32 trials, during which their average reaction times and accuracy level were presented on the screen. Participants were reminded to respond as accurate and fast as possible, and were motivated to respond faster if their average accuracy levels exceeded 90% to prevent ceiling effects in accuracy of performance.

Throughout the entire experiment, eye movements were monitored using a Tobii eye tracker (Tobii AB, Stockholm, Sweden). Gaze data were analyzed online, so that the experimenter could remind the participant to keep fixation in case the participant repeatedly broke fixation during trials.

Procedure

Participants were seated at a 90 cm distance from the computer monitor. Before the start of the experimental task, four minutes of resting state data were recorded. During the resting state EEG recording, participants were asked to alternately watch a central fixation dot and close their eyes for one minute. Onset times for eyes closed and fixation were cued using an auditory cue. This sequence was repeated twice. Analyses of the resting state data were not included in the current report.

After completion of the resting state recording, participants were given extensive task instructions for the change detection task and performed a practice session to become acquainted with the task. The practice session consisted of four practice blocks of 16 trials each. In the first two practice blocks, immediate feedback was given on participants' performance ('correct', 'incorrect', or 'too late'). In the last two practice blocks, there was no trial-wise feedback anymore, similar to the experimental task. Following the practice session, participants continued with the change detection task. Together, the practice and experimental EEG session lasted approximately one hour. At the end of the EEG session, participants were invited for a separate short behavioral session in which we administered a symmetry span task (Unsworth, Heitz, Schrock, & Engle, 2005) to obtain an independent index of participants' complex visual working memory capacity (Conway, Kane, Bunting, et al., 2005).

EEG recording and preprocessing

EEG data were acquired at a sampling rate of 512 Hz using a Biosemi set-up with 64 channels, placed according to the 10-20 system. External reference electrodes were placed on the earlobes, to be used for off-line referencing of the data. External electrodes placed above and below the left eye were used to measure vertical eye movements and blinks (vertical electro-oculogram; VEOG). Electrodes placed at the outer canthi were used to measure horizontal eye movements (horizontal electro-oculogram; HEOG).

Off-line, the EEG data were high-pass filtered at 0.5 Hz, and epoched from -2200 to 5000 ms around stimulus onset. The epoched data was manually inspected and trials with muscle artifacts, as well as blinks during presentation of the flickering placeholders (potentially impeding an SSVEP response) were excluded from further analysis. Gaze data were used to detect trials containing eye-movements during the encoding and maintenance interval of the task (deviations of ≥ 1.5° visual angle away from fixation for 50 consecutive ms or longer). The cleaned datasets for each participant contained 313 trials (SD 43.5 trials) on average (81.4% of the total number of trials in the task; SD 11.3 %).

SSVEP analyses: spatiotemporal filtering

The SSVEP and ongoing spontaneous oscillatory activity usually have overlapping frequency content, impeding separation of the SSVEP based on spectral characteristics of the data alone. In order to optimally extract SSVEPs, we exploited the distinct temporal (frequency) as well as spatial (scalp distribution) characteristics of the SSVEP signal with respect to the ongoing background activity. This was done through rhythmic entrainment source separation (RESS; Cohen & Gulbinaite, 2017). RESS belongs to a family of denoising source separation techniques that can be optimized to extract specific spatiotemporal features of the data (Jaakko, Särelä, & Varela, 2005). RESS comprises the computation of a spatial filter that effectively maximizes the explained variance for a specified feature of the data, in our case the frequency-specific SSVEP signal, relative to a reference signal, in our case broadband ongoing electrophysiological activity. RESS was performed on the concatenated epochs spanning the time window during which the flickering stimuli were presented on the screen (excluding the first 500 ms during which the SSVEP was still building up, resulting in a window of -500 to 2500 ms around stimulus presentation. Power at the SSVEP frequency was isolated by band-pass filtering the concatenated trials using a narrow-band filter centered at the SSVEP frequency of interest (frequency-domain Gaussian filter kernel; FWHM = 0.5 Hz). The broadband EEG data was taken as the reference data. Time-averaged covariance matrices were computed separately for the SSVEP data at the center frequency (S) and the reference data (R). Generalized eigenvalue decomposition of the matrix product $R^{-1}S$ was used to construct frequency-specific spatial filters (RESS components). The eigenvector (i.e., channel weights) with the largest eigenvalue was selected as the spatiotemporal filter at the tagging frequency. This eigenvector (column vector with values representing channel weights) was multiplied by the original channel time series to obtain a component time series. As can be seen in Figure 3a, the frequency content of the resulting component time series is highly specific to the tagging frequencies used.

Given that topographies of SSVEPs may differ across participants and frequencies (Gulbinaite et al., 2014), we computed the spatial filters separately for each participant and flicker frequency. Furthermore, as activity elicited at different stimulus positions may project differently onto the scalp (Vanegas, Blangero, & Kelly, 2015), the procedure described above was performed separately for the 14 unique stimulus configurations used in the experiment by using subsets of trials. This finally resulted in two frequency-specific component time courses for every trial optimized for each flicker frequency and trial-specific stimulus configuration. Note that construction of the spatial filters was done on the condition-average data (collapsed across target vs. distractor locations and distractor load), and was thus independent of potential effects of experimental manipulations.

As the main potential danger of RESS is overfitting (Cohen & Gulbinaite, 2017), resulting in time series reflecting noise instead of SSVEPs, we only included participants for whom inspection of the frequency spectrum of the raw data showed a peak at the SSVEP frequencies on at least one of the 16 most posterior channels. Furthermore, we excluded the most anterior channels prior to RESS to prevent contamination of the component time series by frontal electromyographic (EMG) artifacts at the frequency of interest. RESS was performed using the 43 remaining channels (see Figure 3a). The effect of experimental manipulations on SSVEP amplitude was assessed by comparing SSVEP amplitude across experimental conditions (targets vs. distractors; low vs. high distractor load) and time intervals (encoding 0-500 ms; maintenance 500-2500 ms). Hereto, we performed an FFT on the data and computed the trial-average frequency spectrum for every condition (using a frequency resolution of .1 Hz). In order to avoid an effect of power-law scaling of EEG data on our results, we expressed the power at each flicker frequency as signal-to-noise-ratio (SNR), which was computed as the power at the SSVEP peak relative to the power at neighboring frequencies (averaging the power at frequencies spaced ± .4, .5 and .6 Hz distance from the SSVEP frequency of interest; Vanegas et al., 2015). Given that previous research has shown that attentional modulations of SSVEP amplitude may be restricted to the second harmonic of the SSVEP (Kim et al., 2011), we also examined the presence of attentional modulations of stimulus locations on the second harmonic of the SSVEP (32 and 36 Hz). Hereto, separate spatial filters were constructed and resultant component time series were analyzed as described before. The SNR at 32 and 36 Hz was computed using the average power at neighboring frequencies spaced ± 2, 2.5, and 3 Hz distance from the SSVEP frequency (neighboring frequencies for the harmonics were spaced at a larger distance from the SSVEP frequency to take into account the wider frequency response of the component time series; see Figure 4a vs. 3a). For both the fundamental and harmonic component of the SSVEP, we normalized the condition-specific SNR according to the average SNR for each interval and frequency (Andersen, Fuchs, & Müller, 2011). In the following, whenever we mention SSVEP response, we refer to the normalized SNR of the SSVEP computed as outlined here.

Statistical analyses

Our first prediction was that VSTM performance would be lower on high compared to low distractor load trials. To test this prediction, we examined the effects of our manipulation of distractor load (low vs. high) and probe type (no change; new change; lure change) on accuracy (% correct) and speed (RT in ms) of performance with separate repeated measured ANOVAs. In case of significant effects, follow-up paired t-tests were used to assess the statistical significance of the contrasts of interest. Planned comparisons were used to assess the difference in VSTM performance on lure and new change trials in order to assess color-location binding. All behavioral analyses were computed on the cleaned behavioral data after exclusion of trials containing eye movements, uninformed responses (RTs < 150 ms), and response omissions. Working memory capacity (WMC) was measured as the partial symmetry span score on the symmetry span task (Conway, Kane, & Al, 2005). We expected that effects of distractor load on performance would differ between high- and low-capacity individuals. Therefore, we correlated the effect of distractor load on performance accuracy (distractor costs; decline in % correct for low vs. high distractor loads) with VSTM capacity (measured as average VSTM performance across distractor loads) and WMC (measured on the symmetry span task).

In order to investigate attentional deployment to target and distractor locations during VSTM, we normalized SSVEP amplitudes within each frequency (see previous section) and subsequently collapsed across tagging frequencies (Andersen et al., 2011). Statistical analyses were performed on the correct and cleaned trials only. To determine the effects of attention, we subjected the condition specific normalized SSVEP response (at the fundamental frequency or second harmonic) to a repeated measures ANOVA with the factors location (target; distractor), condition (low; high distractor load), and interval (encoding 0-500 ms; maintenance 500-2500 ms). In case of significant effects, post-hoc t-tests were conducted to test the difference between different levels of the factor of interest. Lastly, as we expected individual differences in the mechanisms involved in attentional filtering (Gaspar et al., 2016; Gulbinaite et al., 2014), we examined whether attentional modulation of target and distractor locations was related to the effect of distractors on behavior by including behavioral distractor costs as a covariate in our analysis. An alpha level of .05 was used as the significance criterion for all statistical analyses.

Data availability statement

The datasets generated during and/or analyzed during the current study are stored in the University of Amsterdam repository, and are available from the corresponding author on reasonable request.

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CHAPTER 5

Oscillatory mechanisms of response conflict elicited by color and motion direction: an individual differences approach

Goal-directed behavior requires control over automatic behavior, for example when goal-irrelevant information from the environment captures an inappropriate response and conflicts with the correct, goal-relevant action. Neural oscillations in the theta band (~6 Hz) measured at midfrontal electrodes are thought to form an important substrate of the detection and subsequent resolution of response conflict. Here we examined the extent to which response conflict and associated theta-band activity depend on the visual dimension that triggers the conflict. We used a feature-based Simon task to manipulate conflict by motion direction and stimulus color. Analyses were focused on individual differences in behavioral response conflict elicited across different stimulus dimensions, and their relationship to conflict-related midfrontal theta. We first confirmed the presence of response conflict elicited by task-irrelevant motion and stimulus color, demonstrating the usefulness of our modified version of the Simon task to assess different sensory origins of response conflict. Despite titrating overall task performance, we observed large individual differences in the behavioral manifestations of response conflict elicited by the different visual dimensions. These behavioral conflict effects were mirrored in a dimension-specific relationship with conflict-related midfrontal theta power on incongruent trials, providing a tight link between midfrontal theta and individual variability in dimension-specific conflict sensitivity. Finally, exploratory analyses of interregional functional connectivity suggested a role for frontoparietal phase synchronization in conflict experienced when color was the task-relevant visual dimension. Highlighting the importance of an individual differences approach in cognitive neuroscience, these results reveal large individual differences in experienced response conflict depending on the source of visual interference, which predict conflict-related midfrontal theta power.

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Introduction

Cognitive control is essential for goal-directed behavior in complex environments. It is particularly important when habitual, automatic behavior interferes with planned actions, for example when irrelevant or distracting information automatically activates a response tendency that will lead to an error (Botvinick, Cohen, & Carter, 2004; Eriksen & Eriksen, 1974; Simon & Wolf, 1963). In such situations, cognitive control is essential to detect conflict between multiple competing responses and override the incorrect action impulse, by biasing neural processing towards the planned action (Miller & Cohen, 2001).

A growing body of work indicates that theta oscillations (4-8 Hz) provide an important neural mechanism through which the need for enhanced cognitive control is signaled, realized, and communicated to other areas in the brain (Cavanagh & Frank, 2014; Cohen, 2014a), and hence critically support flexible goal-directed behavior. In particular, many studies have shown robust conflict-related increases in theta band power at midfrontal scalp sites in the time window between stimulus presentation and execution of a behavioral response (Cohen & Cavanagh, 2011; Hanslmayr et al., 2008; Nigbur, Ivanova, & Stürmer, 2011; Pastötter, Dreisbach, & Bäuml, 2013). Yet, while conflict-related theta power has been observed during perceptual as well as response conflict (Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012), the degree to which conflict-related theta responses depend on the specific source and strength of sensory interference remains presently unknown.

Midfrontal conflict-related theta responses are clearly present at the group level, but are typically also observable at the level of the individual participant (Cohen, 2014a; Cohen & Donner, 2013). Notably, individuals often exhibit variability in conflict-related theta that may systematically relate to variability in other conflict-related neural markers and/or behavioral performance (Cohen & Donner, 2013; Egner, 2011). Such individual differences can thus form an important source of information concerning the underlying constructs and/or circuits involved in the detection and resolution of response conflict (Vogel & Awh, 2008). Indeed, individual differences in conflict-related midfrontal theta power have been shown to relate to individual differences in behavioral indices of conflict adaptation (the effect of recently experienced response conflict on current performance; Pastötter et al., 2013). Furthermore, under conditions of varying conflict probability, probability-related modulations of conflict-related behavior and midfrontal theta responses have been shown to be related across individuals (van Driel, Swart, Egner, Ridderinkhof, & Cohen, 2015). Individual differences analyses relating conflict-related theta responses to individual variation in conflict-related effects on behavior can thus provide important insights into the neural mechanisms underlying conflict detection and resolution.

One precondition for studying individual differences is the presence of variation in the measure of interest across individuals (Vogel & Awh, 2008; Zilles & Amunts, 2013). In the context of response conflict, one potentially powerful way to increase individual variability in response conflict is to equalize the time courses of goal-directed and automatic activation of response tendencies. According to the influential dual-route model for stimulus-response correspondence effects, such as response conflict in Simon tasks (Kornblum, Hasbroucq, & Osman, 1990; Ridderinkhof, 2002; van den Wildenberg et al., 2010), response conflict arises as a consequence of fast direct, automatic response activation by a task-irrelevant stimulus feature, whereas deliberate response decision processes that are associated with goal-directed actions take more time. In most previous research on response conflict, direct response activation typically coincides with fast response activation: Stimulus location in typical Simon tasks leads to rapid activation of the interfering response (Liu, Stevens, & Carrasco, 2007). Possibly, slower automatic response activation results in more similar time courses of direct and deliberate response activation, and hence, fewer fast errors (Burle, van den Wildenberg, & Ridderinkhof, 2005), which potentially allows for early conflict-related modulations of sensory processing prior to response. Tasks in which the task-irrelevant information is accumulated in a more gradual fashion (e.g., by motion direction; Donner et al., 2007; Zavala et al., 2014), may thus provide a more sensitive measure for examining individual differences in experienced response conflict than traditionally used location-based Simon tasks.

In the present EEG study, we exploited individual differences in response conflict induced by distinct visual dimensions (motion-direction and stimulus color) to gain a better understanding of the mechanisms involved in inducing and resolving response conflict, and the generality of these mechanisms to conflict elicited by different sensory dimensions. We further assessed whether dimension-specific response conflict is affected by top-down modulations of sensory processing prior to the time of response. Participants performed a Simon task with colored moving dot patterns (see also Galashan, Wittfoth, Fehr, & Herrmann, 2008; Wittfoth, Buck, Fahle, & Herrmann, 2006) that were always characterized by a motion direction (leftward vs. rightward) and a color (blue or green), while their brain activity was recorded with EEG. At the beginning of each block of 10 trials, participants received an instruction to selectively respond according to one of the stimulus dimensions. On a proportion of trials, the task-irrelevant stimulus dimension would activate the incorrect response hand, resulting in response conflict. This design allowed us to assess the presence and dimension-specificity of response conflict, and the extent to which it is associated with similar theta-band oscillatory dynamics as location-based response conflict (Cohen, 2014a; Cohen & Ridderinkhof, 2013; Nigbur et al., 2011). By leveraging individual differences, we also examined to what extent response conflict is dependent on the stimulus dimension inducing the conflict (color; motion direction), or is instead general across stimulus visual dimensions. Furthermore, we investigated whether individual differences in the effect of response conflict on behavior are similarly predicted by individual conflict-related midfrontal theta power for each stimulus dimension. Finally, we explored the role of sensory modulations in response conflict by examining whether individually experienced response conflict is affected by communication between midfrontal cortex (MFC) and task-relevant sensory regions. To this end, we ran a cross-subjects correlation between dimension-specific conflict-related phase synchronization between MFC and sensory regions prior to the time of response on the one hand, and the dimension-specific conflict-related midfrontal theta response on the other.

We had several predictions. First, we predicted to find response conflict on incongruent trials, reflected in impaired performance on incongruent compared to congruent trials, as well as a transient increase in midfrontal theta power at the time of response, on both attend-color and attend-motion trials. Second, we predicted that individuals who would exhibit a strong conflict-related decline of performance would also show a stronger theta response at midfrontal scalp sites, and predicted that this particular relationship would depend on the source of visual interference (Snyder & Foxe, 2010). Lastly, we hypothesized that strong conflict-related modulation of early sensory activity by medial frontal cortex, as reflected in interregional communication, would reduce response conflict signaling, as indicated by the subsequent conflict-related midfrontal theta response.

Methods

Participants

Twenty-nine participants (M = 22.6 yrs (SD 2.86 yrs); 24 F) participated in this study in return for course credits or monetary compensation. A selection of participants in this experiment also performed an MRI and behavioral session, data from which have been reported elsewhere (van den Brink et al., 2014). Additionally, electromyography (EMG) data from the present EEG study have been reported previously (Cohen & van Gaal, 2014). All participants had normal or corrected-to-normal vision and were right-handed. Participants gave written informed consent prior to participation in the experiment. The experimental procedure was in accordance with relevant laws and institutional guidelines, and was approved by the local ethics committee of the

University of Amsterdam.

Experimental task

Participants performed a visual feature-based Simon task, in which response conflict could be elicited by motion direction and stimulus color (Bosbach, Prinz, & Kerzel, 2004; Galashan et al., 2008; Wittfoth et al., 2006). The task was presented using Presentation software (Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com). On each trial, participants viewed a moving dot pattern that was characterized by one of two different motion-directions (leftward or rightward), and one of two possible colors (green or blue). Subjects were instructed to either indicate the motion direction or the color of the moving dots. The relevant dimension would always change after a block of 10 trials. Prior to the onset of each block of 10 trials, the relevant dimension for the upcoming 10 trials was displayed by presentation of the word 'color' or 'motion' in white letters on a black background (see Figure 1a). Participants were asked to attend to the stimulus dimension presented in the instruction (color or motion), and to identify the color (green or blue; color trials) or motion direction of the dot pattern (leftward or rightward; motion trials). They were asked to indicate their response as fast as possible by using their thumbs to press one of the response buttons attached to the left and right armrests of the chair. On motion trials, participants were asked to

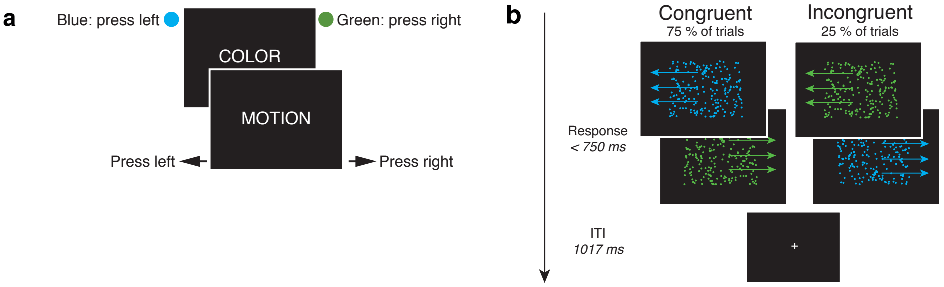

Figure 1. Feature-based Simon task with colored moving dot patterns. A) Participants were asked to attend to the color or motion direction of the moving dot patterns. When attending to stimulus color, participants were asked to respond with a left button press if the pattern was blue, and a right button press if the pattern was green. When attending to motion direction, participants were asked to respond with the response hand corresponding to the motion direction. B) Display of the possible trial types in the task. On 75% of the trials (congruent trials), the task-relevant and task-irrelevant features activated the same (correct) response hand. On 25% of the trials (incongruent trials), the task-irrelevant dimension was associated with a different (incorrect) response hand than the task-relevant dimension, leading to response conflict. The colors and number of dots displayed here do not necessarily resemble the actual stimulus characteristics: Stimuli consisted of 200 moving dots of which a proportion moved coherently to the left or right. All other dots moved in a random direction. The actual color of the dot patterns was titrated such that participants performed correctly on 85% of all trials by adjusting the similarity between blue and green hue. Stimuli were removed from the screen when the participant made a response, or at the end of the response window (750 ms), and followed by an inter-trial interval of (1017 ms).

respond with the hand corresponding to the motion direction of the dots. On color trials, participants were asked to respond with their left hand for blue patterns, and with their right hand for green patterns (the assignment of color to response hand was fixed across participants; see Figure 1a). On each trial, the task-irrelevant stimulus dimension was either congruent with the relevant feature, and thus activated the same response (leftward moving blue patterns; rightward moving green patterns), or was incongruent with the task-relevant feature, and activated the incorrect response hand (leftward moving green patterns; rightward moving blue patterns; see Figure 1a). In total, the task contained 1200 trials. The proportion of incongruent trials was 25% percent, resulting in 300 incongruent and 900 congruent trials per participant. Within each block of 10 trials, congruent and incongruent trials were presented in a random order. For one subject, the experiment contained 106 additional trials compared to the typical 1200 trials included in the experiment, due to a programming error. These additional trials were proportionally sampled from the four conditions and were therefore included in subsequent analyses.

Stimuli consisted of 200 moving dots (.06 degrees visual angle (dva) diameter) presented within a square frame subtending 7.3 by 6.4 dva (note that dva measures are approximate because subjects were not physically constrained during the experiment). A proportion of the dots would move coherently to the right or to the left, whereas all other dots would move in random directions. Throughout the experiment, we attempted to minimize the influence of general task difficulty on conflict experienced by the stimuli across visual features and individuals. To this end, performance was titrated to ± 85% correct throughout the task for each participant (range: 84 – 86%), by adjusting the proportion of coherently moving dots during attend-motion blocks, and by manipulating the similarity between the blue and green hues on attend-color blocks. Yet, as noted in the Results section, this titration procedure did not work as well as predicted in particular for motion direction. Moving dot patterns were removed upon response or at the end of the response window (750 ms). When a participant failed to respond within the response window, an instruction to respond faster was presented for 1000 ms (white letters on black background). Otherwise, participants received no trial-wise feedback on their performance. Responses or the instruction to respond faster were followed by an inter-trial interval (ITI; 1017 ms) during which a white fixation cross (0.2 dva) was presented on a black background (see Figure 1b). Participants were given a short break every 100 trials, in which they received feedback about their average reaction times, in order to motivate them to balance speed with accuracy.

At the start of the experiment, participants were seated in a comfortable chair in a dimly lit room at 90 cm distance from the computer screen. Prior to the start of the EEG recording, participants performed 40 practice trials in which they received immediate feedback about their response. Depending on the participants' timing of the breaks in the practice and experimental session, the total duration of the EEG session was approximately 50 minutes.

EEG: recording, preprocessing and time-frequency decomposition

EEG data were recorded at 512 Hz using a Biosemi set-up with 64 channels placed according to the international 10–20 system. Preprocessing and analysis of the EEG data was performed in Matlab (The MathWorks Inc., Natick, MA, 2000), using EEGlab software (Delorme & Makeig, 2004) and in-house written code (Cohen, 2014b). Additionally, we used external electrodes to record data at peri-ocular electrodes to detect blinks, the left and right thumb muscles to record EMG, and both earlobes for offline referencing. Offline, EEG data were rereferenced and high-pass filtered at 0.5 Hz. Data were epoched from −1.5 to +2.5 s surrounding stimulus onset, and the baseline period (200 ms pre-stimulus) of each epoch was subtracted from the entire epoch. All trials were visually inspected, and trials containing excessive EMG or other artifacts not related to blinks were manually removed. Independent components analysis was computed using EEGLAB software (Delorme & Makeig, 2004), and components containing blinks or other artifacts that could be clearly distinguished from brain-driven EEG signals were subtracted from the data. Trials in which participants made an error, and trials with fast responses (RT < 200 ms), were excluded from further analyses. Finally, a current-source-density (CSD) transformation was applied on the data, which is a spatial filter that increases topographical specificity by effectively subtracting out spatially broad and therefore likely volume-conducted effects (Kayser & Tenke, 2006). This approach has been validated for investigating inter-electrode synchronization (Srinivasan, Winter, Ding, & Nunez, 2007; Winter, Nunez, Ding, & Srinivasan, 2007).

After preprocessing, a stimulus-locked dataset and a response-locked dataset were created in which time zero reflected stimulus presentation and the time of response, respectively. Subsequently, epochs in each dataset were organized according to the four experimental conditions (congruent vs. incongruent; attend color vs. motion). As the experiment contained three times as many congruent compared to incongruent trials, we performed an additional trial selection procedure on the EEG-data to match trial numbers between the two congruent and the two incongruent conditions before further analyses. This was done by RT-matching subsets of n trials (where n reflects the number of trials in the smallest condition) from the three largest conditions to the smallest condition of each individuals' EEG dataset (Cohen, 2014b). This procedure resulted in EEG-datasets with four conditions with equal trial counts and optimally similar RT distributions, ensuring that potential effects of our experimental manipulation in later analyses, particularly in the analysis of connectivity, cannot be attributed to differences in trial count or large differences in response times between conditions (Van de Vijver, Cohen, & Ridderinkhof, 2014).

In order to extract frequency band-specific power reflecting local activity, we analyzed EEG data using time-frequency decomposition for each channel and condition (see e.g., Cavanagh et al., 2009). A time frequency representation of the data was obtained by multiplying the power spectrum of the EEG (obtained through the fast-Fourier-transform) by the power spectrum of complex Morlet wavelets: where *i* is the

$$e^{i2\pi ft}\, e^{-t^2/2s^2}$$

complex operator, ***t*** reflects time, ***f*** reflects frequency (1 to 30 Hz in 20 logarithmically spaced steps), and ***s*** defines the width of each frequency band, set according to ***n***/(2π***f***), where n is the number of wavelet cycles that increased from 3 to 10 in logarithmic steps), of which the inverse fast-Fourier-transform was taken. An estimate of frequency-band-specific power at each time point was defined from the resulting complex signal as the squared magnitude of the result of the convolution (real[z(t)]2+ imag[z(t)]2). After time-frequency decomposition, power was converted to a decibel-scale (dB) transform (dB power = 10*log10[power/baseline]), which enables comparison of amplitude across frequency bands. For dB normalization, we used the frequency-specific, condition-average activity in the time window between 300 and 100 ms before stimulus presentation as a baseline. For computational purposes, data were down-sampled to 40 Hz after time-frequency decomposition (Cohen, 2014b).

Frequency band-specific inter-site phase clustering (ISPC) reflecting interregional connectivity was computed using the stimulus-locked dataset. ISPC was computed according to:

$$\frac{1}{n} * \sum_{t=1}^{n} e^{\,i(\theta jt\, -\, \theta kt)}$$

where *n* is the number of trials, and *θj* and *θk* are the phase angles of electrodes j and k. This yields an index of the consistency of phase angle differences between 2 electrodes at each time-frequency point over trials, which was computed for each possible pair of electrodes and all frequencies (1 to 30 Hz in 20 logarithmically spaced steps). Estimates of ISPC may range from 0 (no phase synchrony between channels) to 1 (identical phase angles between channels). Similar to the power data, data were down-sampled to 40 Hz for computational purposes. Finally, baseline subtraction of ISPC values was performed using the identical time window as used for the power analyses (-300 to -100 ms).

Statistical analyses

All behavioral analyses were performed after removal of trials with response omissions (8-108 trials (M = 38.7) per dataset) or fast responses (RT < 200 ms; 0-8 trials (M = .79) per dataset). The effect of congruency (congruent (C) vs. incongruent (IC)) and stimulus dimension (color vs. motion) on accuracy and speed of responding were assessed using repeated measures ANOVAs. In case of significant main effects or interactions, the statistical significance of differences between factor levels was assessed using follow-up t-tests. The relationship between the conflict effect on accuracy of performance (% correct; C vs. IC) for the two stimulus dimensions (color vs. motion) across individuals was assessed using correlation analyses. An alpha level of .05 was used as the significance criterion.

Statistical analysis of conflict-related oscillatory dynamics was performed using the cleaned and correct trials after removal of fast responses (RT < 200 ms) and trials following a new instruction (first trial of every block). Average theta power (4-8 Hz; Cohen & Ridderinkhof, 2013) was computed for C and IC trials using the response-locked data, collapsed across features (color vs. motion). Since the precise time window of response-conflict in the present motion-based Simon task may be slightly different than in typical location-based Simon tasks, samples showing a significant conflict effect on midfrontal theta power (at channel FCz) were identified using a running t-test across the time window around response (-800 to 800 ms peri response). Significant samples in the observed data were compared against significant samples observed under H_0 through permutation testing. Specifically, samples that showed a significant conflict effect on theta power in the observed data were rejected if they were not part of a cluster (i.e., series of temporally adjacent samples showing a significant conflict effect) that exceeded the cluster size observed under H_0. The cluster size distribution under H_0 was obtained through 1000 permutations on which the data was swapped between conditions (C vs. CI) for a random subset of participants before computation of the test statistic. On each permutation, the largest observed cluster size (i.e., series of consecutive samples showing a statistically significant conflict effect in the permuted data) was selected and saved, rendering a distribution of maximal cluster sizes observed under H_0 (computed separately for clusters showing a negative and positive effect of response conflict on theta power). The cluster size at the 95th percentile of the permuted distribution was used to determine statistical significance of consecutive samples showing a significant condition-difference in the observed data.

The relationship between (feature-specific) behavioral and neural indices of response conflict was addressed by means of cross-subject correlation analyses of (feature-specific) conflict-related decline of performance (% correct; C vs. IC) and dimension-specific conflict-related midfrontal theta power (4-8 Hz; IC vs. C) in the time window showing significant conflict-related theta power across visual dimensions (defined as outlined above).

Finally, we assessed the relationship between individual differences in stimulus-locked interregional communication between sensory and midfrontal areas, and the conflict-related midfrontal theta response. Based on previous research showing effects of attending color vs. motion on parietal (Schoenfeld et al., 2007) as well as occipital (Snyder & Foxe, 2010; Zanto, Rubens, Bollinger, & Gazzaley, 2010) scalp sites, we computed attention-related ISPC between FCz and a cluster of bilateral parietal (P3/4; P5/6; see Figure 4a), and occipital channels (POz; Oz; O1/2) collapsed across visual dimensions, in the time window between 200 and 500 ms post stimulus onset. Analyses were focused on connectivity in the theta and alpha bands (Cohen & Van Gaal, 2013; Zanto et al., 2010). Conflict-related ISPC between frontal and posterior clusters was then related to conflict-related theta power in the time window showing a significant conflict effect or behavior across individuals, separately for each dimension (attending to color vs. motion), using Spearman's correlation coefficient.

Results

Behavior

After preprocessing, the resulting behavioral datasets contained 1160 trials on average (SD 57.7). We assessed whether congruency and attended dimension affected accuracy of performance with a repeated measures ANOVA with the factors congruency (C vs. IC) and visual dimension (color vs. motion). This revealed a main effect of congruency on accuracy (Figure 2 and Table 1), indicating that perceived motion direction and stimulus color automatically induced response conflict on incongruent trials. The effect of visual dimension was also significant, indicating that our attempt to eliminate general differences in task difficulty across visual features did not work out as expected: in particular, participants' average performance on motion trials did not reach the level of 85% targeted during the staircase procedure. In general, responding to motion direction was thus more difficult than responding to stimulus color. Further, the interaction between the effect of congruency and visual dimension was significant, and showed that perceived motion direction has a stronger effect on automatic response activation than the learned association between stimulus color and response hand. Yet, importantly, the main effect of congruency on accuracy of performance suggests that although the size of the conflict effect differed across visual dimensions, the present

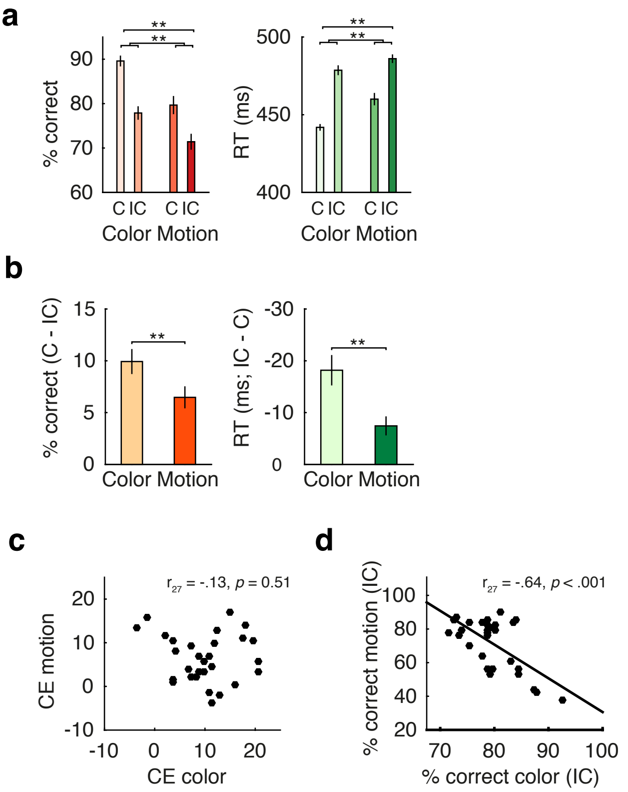

Figure 2. Behavioral performance. A) Group average accuracy of performance (left panel) and response times (RT; right panel) displayed for the different conditions (congruent (C) vs. incongruent (IC); color vs. motion). Accuracy levels were affected by congruency as well as visual dimension, and the effect of congruency and dimension interacted (see C). Similarly, RTs were affected by congruency, visual dimension, and exhibited an interaction between these factors (see C). B) Graphical display of the interaction between the effect of congruency and visual dimension. The effect of congruency was larger on color than on motion trials, both for accuracy and RT. C) The conflict effect (% correct C vs. IC) on color and motion trials was not related across individuals. D) Accuracy of performance (% correct) on incongruent color and motion trials was negatively related across individuals.

feature-based Simon task showed response conflict elicited by task-irrelevant motion direction as well as stimulus color.

Analysis of the effect of congruency and visual dimension on reaction times revealed a comparable pattern (Figure 2 and Table 1), further indicating that response conflict was reliably elicited in our feature-based Simon task.

We next explored whether response conflict (accuracy of performance on congruent vs. incongruent trials) was correlated across the two visual dimensions (attend-color versus attend-motion), but this was not the case (r_{27} = -.13, *p* = .511; see Figure 2c). However, when considering incongruent trials only, performance across the two dimensions was significantly negatively correlated (r_{27} = -.64, *p* < .001). That is, while both color and motion induced response conflict, some participants experienced increased response conflict due to task-irrelevant motion direction, whereas others experienced increased response conflict due to task-irrelevant stimulus color.

Table 2

Effect	Direction	*df*	*F/t*	*p*
Accuracy				
Congruency	C (84 %) > IC (75%)	1,28	28.64	< .001
Dimension	C (85%) > M (75%)	1,28	12.18	.002
Congruency * Dimension	CE C (10%) > CE M (7%)	1,28	4.43	.044
Reaction Times				
Congruency	C (460 ms) < IC (473 ms)	1,28	50.55	< .001
Dimension	C (451 ms) < M (482)	1,28	42.13	< .001
Congruency * Dimension	CE C (18 ms) > CE M (7 ms)	1,28	12.25	.002

EEG power: conflict-related activity and correlation with behavior

We first assessed whether response conflict in the feature-based Simon task evoked conflict-related theta power as in typical location-based Simon tasks. Figure 3a-b shows the group-average topographical and time-frequency representation of midfrontal theta power (4-8 Hz; channel FCz) on congruent and incongruent trials. As can be seen in this figure, a typical increase in midfrontal theta was observed around the time of response (Cohen & Donner, 2013; Nigbur et al., 2012). This increase in theta activity was centered at FCz, in line with the large body of previous research on conflict-related midfrontal theta power using location-based conflict tasks (Cohen & Donner, 2013; Figure 3a). The difference in theta power on congruent and incongruent trials was significant between -175 ms and 200 ms surrounding response (see Figure 3c). This time window was used to isolate theta power for subsequent analyses.

In order to assess the link between behavioral and neural correlates of response conflict, we correlated average conflict-related theta power in the time-frequency window displayed in Figure 3c to the behavioral conflict effect collapsed across visual dimensions. This revealed no evidence for a relationship between dimension-average behavioral conflict effects, and the conflict-related midfrontal theta across individuals (r_{27} = .09, *p* = .611; Figure 3d).

We observed large individual variation in performance on incongruent color vs. motion trials, and therefore next explored whether behavioral and neural measures of response conflict would be related when analyzing this relationship for each visual dimension separately (color vs. motion). To this end, we separately computed midfrontal conflict-related theta power for color and motion trials using the time-frequency window depicted in Figure 3e-f. Conflict-related midfrontal theta power in this time-

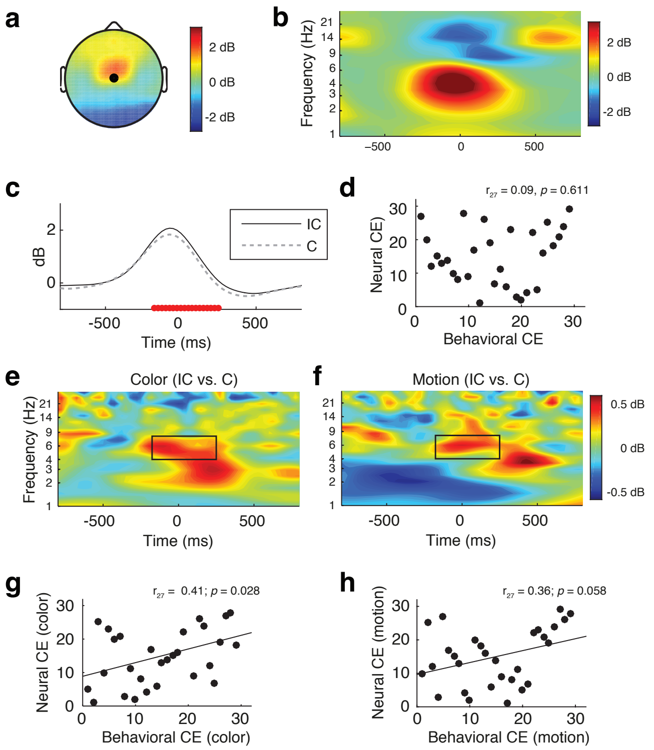

Figure 3. Effects of color- and motion-based response conflict on midfrontal theta power. A) Condition-average midfrontal theta power around the time of response (-100 to 100 ms, where time 0 reflects the time of response). The black circle depicts electrode FCz. B) Time-frequency representation of condition-average activity at FCz. C) Time course of conflict-related midfrontal theta power (4-8 Hz; FCz; incongruent (IC) – congruent (C)), in the time window around response (time 0 reflects the time of response). D) Dimension-average conflict-related theta power (IC - C) is not related to dimension-average conflict effect on performance across individuals. E-F) The conflict effect on midfrontal theta power for color (E) and motion (F) trials. The black outline represents the time window what showed a significant conflict-effect in the feature-average data. As can be seen, the conflict effect is present for color trials (E) and motion trials (F). G) Conflict-related midfrontal theta power on color trials (IC – C) is correlated with the behavioral conflict effect (% correct on C- IC trials) on color trials: Individuals with a larger behavioral conflict effect on color trials, also exhibit a stronger conflict-related theta response on color trials. H) Conflict-related midfrontal theta power on motion trials is correlated at trend level (p = .056) with the behavioral conflict effect (% correct on C - IC trials) on motion trials: Individuals with a larger behavioral conflict effect on motion trials, tended to exhibit stronger conflict-related theta

frequency window was significant on color (t_{28} = 2.13, *p* = .042; see Figure 3e) as well as motion trials (t_{28} = 2.21, *p* = .036; see Figure 3f). To test whether dimension-specific behavioral and neural correlates of response conflict were related across individuals, we subsequently correlated the size of the conflict-related theta response and decline in accuracy of performance across individuals separately for color and motion trials. This revealed a significant positive correlation between conflict-related theta and conflict-related performance decline on color trials (r_{27} = .41; *p* = .028; see Figure 3g), and a marginally significant correlation on motion trials (r_{27} = .36, *p* = .058; see Figure 3h). Thus, participants who showed a larger conflict effect on behavior, also showed a larger effect of conflict on midfrontal theta at the time of response, but this relationship was only present when taking individual differences in dimension-specific performance into account.

EEG connectivity

We next examined if interregional communication associated with selective modulations of color or motion processing would predict response-conflict. To this end, we examined whether stimulus-locked interregional connectivity (inter-site phase clustering; ISPC; Cohen, 2014b) between FCz and posterior sites (see Figure 4a-b) predicted subsequent conflict effects on midfrontal theta power. At the group level, feature-average ISPC between frontal and posterior clusters was selective to the parietal cluster in the time window between 200-500 ms post-stimulus (t_{28} = 1.84,

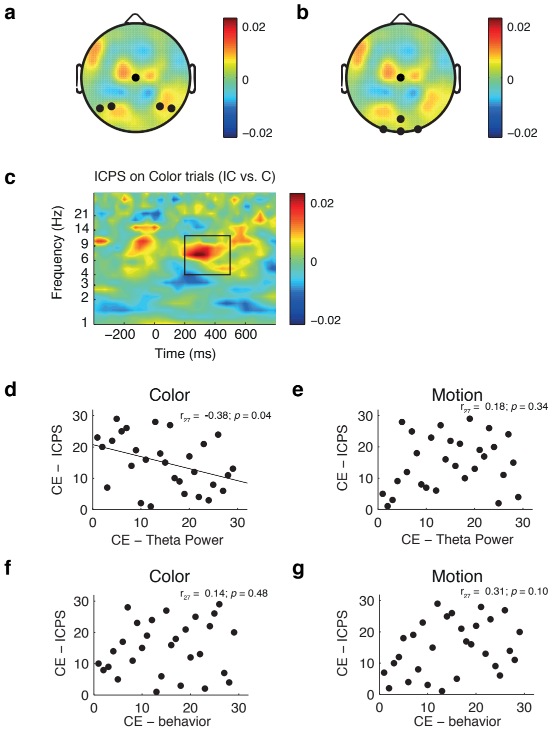

Figure 4. Stimulus-locked, conflict-related inter-site phase clustering (ISPC) between FCz and parieto-occipital sites (IC vs. C; collapsed across visual dimensions). A) Topographical display of conflict-related stimulus-locked ISPC seeded at FCz, and the channels used for the parietal seed. B) Topographical display of conflict-related stimulus-locked ISPC seeded at FCz, and the channels used for the occipital seed. C) Stimulus-locked, conflict-related ISPC between FCZ and parietal sites (P3/4, P5/6) collapsed across visual features. There is significant conflict-related frontoparietal ISPC between 200 and 500 ms post stimulus presentation spanning the theta and alpha band. D) The conflict effect on midfrontal theta power (IC vs. C) on color trials and the conflict-related frontoparietal ISPC on color trials were significantly related across individuals. Individuals with stronger conflict-related frontoparietal ISPC preceding response, showed a smaller conflict effect as reflected in midfrontal theta power. E) Conflict-related frontoparietal ISPC on motion trials did not predict the conflict effect as reflected in midfrontal theta power on motion trials across individuals. F) Conflict-related frontoparietal ISPC on color trials did not predict the behavioral conflict effect (% correct on C vs. IC) on color trials. G) Conflict-related frontoparietal ISPC on motion trials did not predict the behavioral conflict effect (% correct on C vs. IC) on motion trials.

p = .05; see Figure 4c): There was no significant conflict-related synchrony between FCz and the occipital cluster (t_{28} = .73, *p* = .23). We next explored whether across individuals, dimension-specific conflict-related ISPC between FCz and the parietal cluster was related to the dimension-specific conflict-related midfrontal theta response. To this end, we correlated conflict-related frontoparietal ISPC between 200-500 ms following stimulus presentation, to conflict-related midfrontal theta power (in the time window that showed a significant effect of conflict; -175 to 200 ms peri response) across individuals, separately for each visual dimension (attend color vs. motion direction). This analysis revealed a negative correlation between conflict-related frontoparietal ISPC and conflict-related midfrontal theta power when attending to color (r_{27} = -.38, *p* = .04; see Figure 4d), but not when attending to motion direction (r_{27} = .18, *p* = .34; Figure 4e). These findings may indicate that conflict-related frontoparietal ISPC selectively reduces conflict-related midfrontal theta power on incongruent color trials. Indeed, conflict-related frontoparietal ISPC differentially affected subsequent midfrontal conflict-related theta responses on incongruent color and motion trials: The correlation between conflict-related frontoparietal ISPC and midfrontal conflict-related theta power was significantly different across visual features (Z = 2.10, *p* = .04).

To follow up on the correlation between conflict-related frontoparietal ISPC and midfrontal theta, we subsequently correlated conflict-related frontoparietal ISPC prior to response to the behavioral conflict effect for each visual dimension, and found that frontoparietal conflict-related ISPC did not predict the behavioral conflict effect on either color (r_{27} = .14, *p* = .48) or motion trials (r_{27} = .31, *p* = .10; see Figure 4f-g). In summary, the present findings on conflict-related ISPC provide tenuous evidence for a functional relationship between pre-response frontoparietal communication and conflict-related midfrontal theta when attending to color, but not when attending to motion direction (Zanto et al., 2010).

Discussion

In the present EEG study, we exploited individual differences in behavioral and oscillatory markers of color and motion-induced response conflict to determine the extent to which response conflict is stimulus dimension-dependent, and to elucidate the neural mechanisms associated with the detection and resolution of dimension-based response conflict. We observed motion-induced response conflict in incongruent color trials on which motion direction was task-irrelevant, corroborating previous research demonstrating response conflict during motion-based response-activation (Bosbach et al., 2004; Galashan et al., 2008; Wittfoth et al., 2006), and additionally observed color-induced response conflict when color was task-irrelevant. Time-frequency analyses of the EEG-data and our individual differences approach provided three important contributions to the literature. First, time-frequency analysis of EEG data revealed that motion- and color-based response conflict are associated with typical oscillatory signatures of response-conflict, i.e., increased conflict-related theta power at midfrontal scalp sites at the time of response (Cohen, 2014a; Cohen & Donner, 2013; Cohen & Ridderinkhof, 2013; Nigbur et al., 2012, 2011).

Second, behavioral performance on incongruent color and motion trials was negatively correlated across individuals, indicating that the ability to perform a goal-relevant action in the presence of interfering information depends on the strength of interference, which varies across visual dimensions differentially for different individuals. These individual differences were paralleled in a dimension-specific relationship between behavioral conflict effects and conflict-related midfrontal theta power across individuals, while the behavioral conflict was not related to conflict-related theta power when collapsing across visual dimensions. Experienced response conflict thus does not necessarily reflect a generic phenomenon that remains constant across situations, but is at least partially dimension-specific.

Third and lastly, exploratory analyses provided evidence for a dimension-dependent relationship between early stimulus-related frontoparietal phase-synchronization and response conflict, as reflected in dimension-specific midfrontal conflict-related theta power. Increased interregional communication predicted a reduced conflict-effect when attending to color, but not when attending to motion direction. In summary, these results provide important novel insights into the extent to which response-conflict may vary depending on the degree of interference experienced by sensory information activating the incorrect response, and the oscillatory mechanisms involved herein.

Feature-based response conflict is reflected in midfrontal theta activity

The feature-based Simon task used in the present study in which response conflict was induced by either the color or motion direction of colored moving dot patterns elicited typical response conflict, as reflected in slower and less accurate performance when the task-irrelevant visual feature activated the incorrect response hand (Lu & Proctor, 1995; Simon & Wolf, 1963). Previous research on the neural mechanisms involved in the detection and resolution of feature-based response conflict has revealed an effect of motion-based response conflict on the P300 (Galashan et al., 2008), and BOLD-activation patterns in the anterior cingulate cortex (ACC; Wendelken, Ditterich, Bunge, & Carter, 2009; Wittfoth et al., 2006). To the best of our knowledge, the present study is the first to report direct evidence for the oscillatory correlates of feature-based response conflict, reflected in a typical conflict-related transient increase in midfrontal theta power (Cohen, 2014a; Lu & Proctor, 1995). This observation supports the notion that midfrontal theta power serves as a domain-general mechanism through which response conflict is detected and subsequently resolved (Cavanagh & Frank, 2014; Cohen, 2014a; Nigbur et al., 2011).

Individual differences in response conflict depend on feature-specific interference

Interestingly, results from individual differences analyses indicated that response conflict and associated theta activity also depend, at least in part, on the conflict-inducing visual dimension. Performance on incongruent color and motion trials was negatively correlated across individuals, indicating that individuals who experienced a large conflict effect for one task-irrelevant dimension showed a smaller conflict effect when the other dimension was task-irrelevant, and vice versa. The inverse relationship between performance on incongruent color and motion trials is in line with the notion of biased competition in feature-based attention (Polk, Drake, Jonides, Smith, & Smith, 2008), and corroborates previous reports showing that individuals who exhibit improved color perception display relatively impaired motion perception (Banissy et al., 2013; McCarthy & Caplovitz, 2014). The present findings also concord with earlier work using a Navon global-local interference task showing that some individuals suffered from interference when global stimulus features were task-irrelevant whereas in others, local features yielded stronger interference (Richard Ridderinkhof & van der Molen, 1995): EEG analyses revealed that whichever was the ‘dominant’ level incurred neural measures of response conflict at the primary motor cortex. Furthermore, a previous study on the effect of attention to stimulus color vs. motion direction on alpha power modulations (Snyder & Foxe, 2010) found that alpha power modulations sensitive to the attentional manipulation (attend color vs. motion direction) dissociated between subgroups of participants. Whereas one group of participants selectively exhibited alpha power modulations when attending to motion direction, but not color, the other group of participants showed the opposite pattern. Furthermore, for a given subject, the observed alpha power modulations were selective to the visual dimension that was easiest to discriminate, and presumably most likely to cause interference (Snyder & Foxe, 2010). These and the present findings suggest that individuals differ greatly in the extent to which they are sensitive to stimulus color or motion direction, which in turn results in large inter-individual differences in response conflict experienced by each of these visual dimensions when irrelevant to the task at hand.

The observed negative relationship between behavioral performance on incongruent color and motion trials across individuals in the present study was mirrored in a dimension-specific cross-subject correlation between the conflict effect on behavior and midfrontal theta power, providing further evidence that individual differences in experienced response conflict are dependent on processing of sensory information. This result complements previous observations of a within-subject relationship between inter-trial variability in conflict-related theta dynamics and behavior (Cohen & Cavanagh, 2011; Cohen & Donner, 2013; van Driel et al., 2015). Specifically, the present findings reveal that, when taking individual differences in sensitivity to dimension-specific interference into account, the effect of response conflict on behavior and theta power are not only related within, but also across individuals. Previous research has demonstrated that such individual differences in conflict-related behavioral dynamics depend of individual differences the structure of task-relevant brain regions and pathways (Forstmann et al., 2008; van Gaal, Scholte, Lamme, Fahrenfort, & Ridderinkhof, 2011). The results reported in this study suggest that response conflict not only depends on individual differences in brain anatomy, but also depends on individual differences in sensitivity to the sensory information inducing the response conflict.

Conflict-related sensory modulation of interregional communication

Exploratory analyses revealed that conflict-related phase synchronization between midfrontal and parietal sites time-locked to stimulus presentation negatively predicted midfrontal conflict-related theta power at the time of response on color, but not motion trials (see also Zanto et al., 2010). To our knowledge, this study is amongst the first to report stimulus-locked conflict-related modulations of interregional communication that affect experienced response conflict. Existing work selectively reported increased interregional phase synchronization as a function of conflict-related adaptations following incongruent trials (Oehrn et al., 2014; Pastötter et al., 2013; van Driel et al., 2015), but evidence for the involvement of a relationship between conflict-related modulations of interregional communication and conflict experienced on the same trial is still limited.

The observed relationship between conflict-related frontoparietal ISPC and midfrontal theta power on incongruent color, but not motion trials, may indicate that conflict-related ISPC reflects interregional communication of goal-relevant color information: There is evidence suggesting that conflict caused by conflicting perceptual input is primarily resolved through attentional enhancement of goal-relevant information, rather than suppression of irrelevant information (Egner & Hirsch, 2005; Purmann & Pollmann, 2015). On the other hand, the observed conflict-related phase synchronization on color trials may also reflect diminished interregional communication of task-irrelevant information (Palva & Palva, 2011). Given the absence of a link between conflict-related frontoparietal ISPC and behavioral performance, the present findings leave unclear what information is communicated through the observed conflict-related frontoparietal phase synchronization. The precise role of the observed conflict-related interregional phase synchronization thus needs further attention in future studies.

Surprisingly, the present results revealed no relationship between conflict-related interregional communication and the effect of response conflict on midfrontal theta when participants attended to motion direction. This could be due to the fact that motion processing primarily relies on activity along the dorsal stream (Donner et al., 2007; Snyder & Foxe, 2010), which may be more difficult to measure using sensor-level EEG. Furthermore, interregional communication directed at the reduction of response conflict likely also involves subcortical regions (Aron, Herz, Brown, Forstmann, & Zaghloul, 2016; Herz et al., 2017; Zavala et al., 2014). Potentially, sensory modulations following detection of conflicting sensory information are in part transmitted through subcortical routes, which complicates their measurement using scalp EEG.

Summary

The present study revealed robust motion- and color-based response conflict, which was associated with increased theta activity over midfrontal scalp sites. Moreover, large individual differences were observed in the extent to which stimulus color and motion direction elicited response conflict: Individuals who suffered from interference by task-irrelevant motion direction were less prone to interference by task-irrelevant stimulus color, and vice versa. These individual differences were mirrored in conflict-related midfrontal theta responses, indicating that midfrontal conflict-related theta power is involved in domain-general conflict detection and/or resolution, but depends of the sensory source inducing the conflict. Finally, preliminary evidence was found for a role of early frontoparietal communication in resolving response conflict when attending to stimulus color. In conclusion, the present findings provide important insights into response conflict elicited by different visual dimensions and the oscillatory mechanisms involved.

CHAPTER 6

Summary and Discussion

Aims of the current thesis

The main aim of the research presented in this thesis was to determine the role of visual selective attention in goal-directed behavior. It is well known that selective attention can prioritize processing of goal-relevant information through selective enhancement of relevant information processing and suppression of irrelevant information processing. Yet, if, and how, these attentional mechanisms also provide a foundation for Visual Short-Term Memory (VSTM) and response selection is still less clear. In chapters 2, 4 and 5, I addressed the question whether efficient VSTM performance and response selection rely on enhancement of goal-relevant information, or may (also) require suppression of irrelevant processing, and used EEG to measure how these different mechanisms are implemented in the brain. In chapters 3 and 4, I additionally investigated the temporal dynamics of attention during VSTM to determine whether attention continues to play a role during VSTM maintenance, and whether it does so by sequentially rehearsing information. In Chapter 5, I investigated to what extent successful response selection also relies on modulations of sensory information processing. Across chapters, I focused on individual differences in these mechanisms that were predictive of performance, in order to establish the functional importance of the neurophysiological mechanisms involved. In the following sections I will first summarize the main findings from the studies reported in this thesis. I will then discuss the presented findings in light of existing literature and contemporary cognitive neuroscience theories of attention, VSTM and cognitive control. I will conclude by delineating important avenues for future research.

Summary of the main findings

In the present thesis, I set out to investigate whether, and how, selective attention influences short-term memory and goal-directed action, and examined the neurophysiological mechanisms involved. The research described in chapters 2, 3 and 4 aimed to determine the extent to which VSTM relies on attentional modulations of sensory activity. In chapter 2, I examined the role of alpha oscillatory activity during VSTM in the presence of distractors. While many studies have shown an important role for posterior alpha power modulations in proactive attentional filtering during perception (Klimesch, 2012; Payne & Sekuler, 2014), whether or not alpha activity also plays a role in different types of attentional filtering during VSTM was still unresolved, specifically during attentional filtering in more complex visual scenes. Our findings provided selective evidence for the involvement of occipital alpha activity during proactive, but not reactive distractor filtering during VSTM. Corroborating the finding that alpha activity can proactively, but not reactively filter distraction during VSTM, the results from our behavioral and ERP analyses showed that anticipated (and proactively filtered) distractors did not influence performance, whereas unexpected distractors (that required reactive suppression) did. Yet, alpha activity during proactive distractor filtering did not scale with the number of distractors, raising the possibility that the observed alpha power modulations primarily serve as a general routing mechanism to bias information processing to task-relevant sensory regions, but are not involved in suppression of distractors per se. An important question raised by the study described in chapter 2 is thus which neural mechanisms may underlie representation-specific, and/or reactive suppression of unanticipated distraction during VSTM, in order to protect performance.

To address this question, in chapter 4, I investigated whether suppression of distraction during VSTM relies on modulations of stimulus-specific sensory representations (Gaspar, Christie, Prime, Jolicœur, & McDonald, 2016; Noonan et al., 2016). While participants performed a VSTM change detection task with three targets and three distractors, we presented flickering placeholders at individual target and distractor locations to elicit target- and distractor-specific Steady-State Visual Evoked Potentials (SSVEPs). SSVEP responses have been shown to increase with attention (Muller, Bartelt, Donner, Villringer, & Brandt, 2003). The SSVEPs at individual stimulus locations thus allowed us to continuously and simultaneously track attentional modulation of relevant and irrelevant representations during VSTM encoding and maintenance. Results of chapter 4 showed increased attention to target compared to distractor representations, as reflected by enhanced SSVEP responses at target versus distractor locations, thus revealing differential attentional modulation of relevant and irrelevant sensory representations during VSTM. Furthermore, this differential modulation of target compared to distractor representations was functionally important in that it affected VSTM performance. Specifically, attentional differentiation between target and distractor SSVEP responses during VSTM maintenance predicted the effect of distractor load on VSTM performance. That is, individuals who showed increased differentiation of attention to target and distractor representations suffered less from the presence of distractors. Suppression of unanticipated distractors during VSTM thus relies, at least in part, on ongoing attentional modulation of sensory representations of the targets and distractors.

Another outstanding question concerns the temporal dynamics of selective attention during VSTM (Gazzaley & Nobre, 2012). It remains presently unclear whether attention is selectively involved during VSTM encoding, or continues to be important to keep stored information in an active state during VSTM maintenance. In chapters 3 and 4, I examined whether selective attention not only plays an important role in encoding the contents of VSTM, but also continues to support VSTM performance during postperceptual maintenance stages (Awh et al., 1999; Postle, Awh, Jonides, Smith, & D’Esposito, 2004). In chapter 3, we showed that during VSTM in the absence of distraction, attention continues to modulate representations corresponding to stored memory items, as reflected in ongoing amplitude modulations of the SSVEPs elicited at (formerly) relevant locations. Importantly, these attentional modulations were selective to relevant, (to-be) encoded representations, but were absent at task-irrelevant locations, confirming the representation-specificity of the observed attention effects. Furthermore, attentional modulations during encoding were functionally relevant, as reflected in a relationship between attentional modulation of stimulus representations during VSTM encoding and VSTM performance. This is notable because in the presence of distractors, as described above, attentional modulations during VSTM maintenance, but not encoding, predicted behavioral effects of distractor load on VSTM performance. This discrepancy could indicate that the temporal window during which attention is important for VSTM performance is different in the presence versus absence of distraction. Yet, the observed difference may also be attributable to differences in task design across studies, which I discuss in the section below. A final exciting finding from chapter 3 was that we observed first evidence for sequential rehearsal of stored representations, reflected in lagged correlations between SSVEP amplitude modulations across relevant locations. Importantly, the attentional modulations in chapter 3 and 4 were observed during typical VSTM and were not the result of explicit attentional retrocues, which have thus far been used to probe the role of attention during VSTM

(Souza & Oberauer, 2016). Together, the results from chapter 3 and 4 thus provide convincing evidence for ongoing and representation-specific sensory modulations that support VSTM performance.

In chapter 5, we found support for the notion that attentional filtering of distraction, as reflected by modulation of sensory processing, also facilitates response selection. In this chapter, we measured EEG while participants performed a feature-based Simon task in which they attended a colored moving dot pattern. Across blocks, participants either responded to the motion direction or the color of the dot pattern. On a proportion of trials, the irrelevant dimension would activate the incorrect response, leading to conflict during response selection. One key finding of this study was that individuals who showed stronger interference by one task-irrelevant dimension during response selection, were less impaired by the other task-irrelevant dimension, and vice versa. Response selection may thus not be a general phenomenon that solely depends on the efficiency of conflict resolution mechanisms, but is also at least partly dependent on the specific source of interference, which may in turn differ across individuals (Ridderinkhof & van der Molen, 1995; Snyder & Foxe, 2010). Furthermore, the dimension-specific effects of response conflict on behavior were related to individual dimension-specific, conflict-related theta power at the time of response. Hereby, results from chapter 5 corroborate the notion that theta power functions as a domain-general mechanism involved in conflict-resolution (Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012), but at the same time reveal that the recruitment of reactive control mechanisms in part depends of individual differences in sensory processing of competing stimulus features.

Together, the findings presented in this thesis suggest that attention not only supports VSTM through selective encoding of goal-relevant information, but also continues to support VSTM during subsequent maintenance stages. Results from the presented research revealed that at the neural level, alpha activity is predominantly involved in biasing information processing between task-relevant and task-irrelevant regions, whereas attentional modulation of representation-specific sensory activity is particularly relevant for accurate VSTM performance. Furthermore, during response selection, biasing of task-irrelevant sensory processing can also contribute to minimization of response conflict, resulting in more effective goal-directed behavior. In the following, I will consider the reported findings in light of existing literature, discuss limitations of the presented studies, and provide several suggestions for future research that may further our understanding of how selective attention supports goal-directed behavior.

General Discussion

In the introduction of this thesis I illustrated the importance of selective attention for goal-directed behavior with an example that illustrated how even simple tasks in everyday life are crucially dependent of the presence of core cognitive abilities, such as selective attention and visual short-term memory (VSTM). Buying a jar of jam in the supermarket for example, requires the ability to focus on relevant information (e.g., the labels of the jars), and ignore other irrelevant information in the environment (e.g., the shape of the jars, or jars of honey placed next to the jam) that may otherwise needlessly occupy the brain's processing capacity, or may activate an unplanned action (i.e., grabbing a jar of honey instead). Secondly, it is important to be able to remember which varieties of jam are on the shelf while exploring all available flavors, in order to be able to make a deliberate choice and select the preferred jar of jam. Clearly, it would have been impossible to achieve the intended goal of buying the jar of choice without being able to selectively attend and store perceived information. In the present thesis, I investigated these two abilities in the laboratory while recording brain activity from participants with EEG, to gain more insights into the role of these cognitive functions for goal-directed behavior, and the neural mechanisms involved. Specifically, I addressed two important outstanding questions. First, I investigated whether attention supports the ability to temporarily store information by means of attentional modulations of sensory activity. Going back to the example, does it help to enhance visual processing of the labels, or is it (also) important to minimize visual activity corresponding to processing the shape of the jars? Secondly, I studied the time course of the involvement of attention during VSTM, to determine whether attention is primarily important when encoding information in VSTM, or is also important to accurately maintain representations of information in VSTM. In other words, is selective attention only helpful while scanning the shelves, or is attention also required to keep an active memory of what you saw on the shelf before? In the present thesis, these questions were approached from an individual differences perspective, such that individual variation in cognitive performance was used to reveal the neural mechanisms involved. In the discussion below I will discuss the answers to these questions that emerged from the present thesis in light of the existing literature.

Does attention improve VSTM and response selection by means of sensory modulations?

The first question that was addressed in the present thesis concerned the extent to which attentional filtering during VSTM relies on attentional modulations of sensory activity. At the neural level, frontoparietal networks and the basal ganglia have been shown to be important for filtering information that is eventually stored in VSTM (Baier et al., 2010; McNab & Klingberg, 2008). Yet, influential theories posit that VSTM may also rely on local modulations of sensory activity (Ester, Serences, & Awh, 2009; Zelinsky & Bisley, 2015). In order to elucidate the role of selective attention on sensory processing during VSTM, in chapter 2, 3 and 4 I examined to what extent VSTM relies on attentional modulations of alpha activity and representation-specific activity in sensory regions.

VSTM relies on attentional modulation of representation-specific sensory activity

A key finding in this thesis is that both VSTM encoding and maintenance are supported by representation-specific sensory modulations, as reflected by attentional modulations of SSVEPs elicited by placeholders presented at stimulus locations. During VSTM encoding and maintenance of multiple simultaneously presented items (chapter 3), attention selectively enhanced goal-relevant, but not irrelevant sensory representations. Furthermore, attentional modulation of relevant versus irrelevant representations during encoding was predictive of VSTM performance. In the presence of distraction (chapter 4), increased attention to relevant compared to distractor representations was observed throughout VSTM encoding and maintenance. Moreover, across individuals, differential attentional modulation of relevant compared to distractor representations during VSTM maintenance was predictive of behavioral distractor costs: Participants who showed a larger difference in attentional deployment to target compared to distractor locations, showed reduced distractor costs. Results from chapter 3 and 4 thus emphasize that the widely recognized importance of selective attention for VSTM (Gazzaley, 2011) is at least partially reliant on persistent attentional modulation of representation-specific sensory activity.

Present knowledge of the neural principles underlying attentional filtering of irrelevant information is still limited (Adam & Vogel, 2016). Specifically, as mentioned above, while fMRI research has pointed out the involvement of the basal ganglia and prefrontal cortex in attention filtering during VSTM (Baier et al., 2010; Fiona McNab & Klingberg, 2008), the degree to which attentional filtering also supports storage of information in VSTM by modulating sensory activity remained less clear. Initial evidence for the notion that VSTM maintenance requires sustained activity in sensory, representation-specific regions was observed in the form of persistent delay activity in single neurons in macaque primary visual cortex during maintenance of information in VSTM, suggesting that memory traces rely on sustained activity in sensory regions involved in perception of the memorandum (Supèr, Spekreijse, & Lamme, 2001; Woloszyn & Sheinberg, 2009). While invasive recording studies indicated that the portion of neurons that remains persistently active during VSTM maintenance may be relatively small (Kornblith, Quian Quiroga, Koch, Fried, & Mormann, 2017; Woloszyn & Sheinberg, 2009), the recent rise of studies using MVPA to decode sensory activity in fMRI data has led to a vast expansion of findings revealing the presence of mnemonic, item-specific representations in visual cortex during VSTM, that are even detectable at the population level (Emrich, Riggall, LaRocque, & Postle, 2013; Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009). Yet, most of these studies used designs in which only one or two (highly distinct) items were present, or in which multiple items were presented sequentially. These studies thus left unclear whether VSTM of more complex visual displays, that require simultaneous encoding and storage of multiple items in face of distraction, similarly relies on modulations of sensory activity. Results from chapter 3 provide novel evidence for the involvement of persistent sensory modulations during the simultaneous maintenance of multiple items in VSTM.

Previous evidence for the importance of memory-specific persistent sensory modulations during VSTM is based on findings showing that disruption of memory-related sensory activity by presentation of task-irrelevant distractors during the delay period is disruptive for decoding and/or memory performance (Bettencourt & Xu, 2015; Rademaker, Bloem, De Weerd, & Sack, 2015; van de Ven, Jacobs, & Sack, 2012). Yet, while performance or decoding decrements following the presentation of these distractors may indeed indicate that disruption of memory-specific sensory activity impairs VSTM maintenance, they could also result from more unspecific interference or noise caused by the task-irrelevant distractor. Our approach of using SSVEPs to probe stimulus-specific sensory representations in VSTM in chapter 3 and 4 enabled us to assess the presence and functional importance of sensory modulations without disturbing ongoing memory performance, demonstrating that the observed sensory modulations are inherent to typical VSTM maintenance. Importantly, we were able to continuously track sensory modulations of up to six individual locations by tagging each location with a unique frequency. This demonstrates the usefulness of SSVEPs in simultaneously tracking attention to multiple locations.

The involvement of sensory regions in VSTM is in line with the increasingly popular sensory recruitment hypothesis, which posits that memory representations are at least partially stored in the regions processing the stored information during perception (Serences et al., 2009; Sligte, Scholte, & Lamme, 2009). In line with this hypothesis, the close link between attention and VSTM has been proposed to rely on shared attentional priority maps in task-relevant cortical regions, in which task-relevant information is weighed differently than task-irrelevant information (Zelinsky & Bisley, 2015). Importantly, this latter account holds that eventually, all task-related representations are transformed into a spatial priority map, such that features and locations are necessarily bound during VSTM. This notion is particularly relevant in light of the attentional modulations reported in chapter 3 and 4 that were measured as modulations of the SSVEP response elicited at different spatial locations. In these studies, stimulus location was important for VSTM performance because colors had to be bound to location to be able to accurately respond to the probe. Thus, even though attentional selection was initially based on stimulus-shape (chapter 3), in combination with distractor color similarity (chapter 4), as proposed by Zelinsky and Bisley, these feature-based attentional modulations were eventually transformed into modulations of spatial attention.

A notable difference between the findings reported in chapter 3 and 4 is that during VSTM in the absence of distraction (chapter 3), attentional modulations during encoding predicted VSTM performance, whereas in the presence of distraction (chapter 4), attention during maintenance predicted VSTM performance. This pattern could reflect that the time course of the functional role of attention for VSTM is dependent on the presence of distraction, but could also simply reflect differences in experimental design. The encoding interval in the change detection tasks used in chapter 4 was shorter than the encoding interval used in chapter 3 (500 vs. 1000 ms, respectively), rendering it possible that encoding-related attentional modulations shifted to the maintenance period in chapter 4. An alternative explanation for this discrepancy in findings is that distractor suppression commences after initial identification and selection of the distractor stimuli, and thus only becomes apparent later in time, i.e., after encoding, during maintenance. Future research is necessary to dissociate between these different possibilities.

Another important question for future research concerns the neural origin of the attentional modulations observed in chapter 3 and 4. The representation-specific modulations observed in chapter 3 and 4 appeared to be predominantly sensory in nature: the SSVEP amplitude modulations were strongest at occipital scalp sites and were topographically specific, suggesting these representations originated from lower level visual areas. This would be in line with findings showing that some neurons in monkey inferior temporal cortex and V1 remain persistently active during VSTM maintenance (Supèr & Ran, 2008; Supèr et al., 2001; Woloszyn & Sheinberg, 2009). Yet, a recently proposed hypothesis holds that VSTM relies on 'distributed codes' that are not restricted to sensory regions but extend to a variety of brain regions, including parietal and frontal cortex (Christophel, Klink, Spitzer, Roelfsema, & Haynes, 2017; Serences, 2016). The notion that VSTM also depends on persistent activity outside of sensory regions is supported by findings from a recent invasive study showing that a small portion of neurons in the medial temporal cortex continues to represent a memory item by means of sustained firing during maintenance, even in the presence of interfering information (Kornblith et al., 2017). These codes may function as duplicates of the sensory, item-specific representations, providing a buffer that prevents interference by the processing of novel task-irrelevant distraction in sensory regions (Christophel et al., 2017; Kornblith et al., 2017), or serve as perception-action representations that facilitate behavior (Myers, Stokes, & Nobre, 2017). Furthermore, the observed sensory modulations in the present study were conceivably under top-down control by other regions of the brain. Possibly, top-down control is implemented by frontoparietal regions such as the frontal eye fields, that may contain representations of the current task set or behavioral current goals and are known to modulate sensory processing (Armstrong, Chang, & Moore, 2009; Clark, Noudoost, & Moore, 2012; Marshall, Bergmann, & Jensen, 2015). The prefrontal cortex and basal ganglia have also been shown to be involved in attentional filtering (Fiona, McNab & Klingberg, 2008), and may likewise be important for inducing distractor-related modulations of sensory activity, as observed in chapter 4. Finally, subcortical regions such as the thalamus also contribute to selective attention (LaBerge, 1990; Saalmann & Kastner, 2011; Saalmann, Pinsk, Wang, Li, & Kastner, 2012), and are potentially also involved in modulations of sensory activity during VSTM. Future research on the degree to which activity across networks in the brain represents stored information during VSTM is necessary to draw a more complete understanding of how attentional filtering and VSTM storage interact at the network level.

Recently, however, the long prevailing notion that VSTM maintenance relies on persistent sensory activity has been challenged by accounts suggesting that VSTM does not rely on persistent sensory activity, but instead resides in temporally dynamic and ‘activity silent’ codes (Stokes, 2015). This account posits that memory representations are represented in silent or hidden states, i.e., states that are not picked up by population level measurements of brain activity using non-invasive techniques such as EEG and fMRI. Instead, these hidden states are proposed to reside in functional connectivity patterns that may, for example, be expressed in activity-dependent short-term synaptic plasticity (Mongillo, Barak, & Tsodyks, 2008), or phase synchronization of oscillatory activity among task-relevant brain-networks (Salazar, Dotson, Bressler, & Gray, 2012). Furthermore, these states and their network configurations are proposed to dynamically change over time.

At first sight, this account appears at conflict with the observed persistent representation-specific SSVEP modulations during VSTM maintenance in chapter 3 and 4 of this thesis, which are indicative of persistently active, representation-specific neural activity in sensory regions. Yet, when adopting the perspective of activity-silent codes on these findings, the ongoing attentional modulations of SSVEPs may not reflect persistently active memory codes, but may instead reflect the brain's response to an impulse ('ping'; Wolff, Jochim, Akyürek, & Stokes, 2017) (i.e., the flickering stimuli), or the rapid transition of a memory code from an activity-silent state to an active state (Myers et al., 2017), both of which could have revealed the hidden state by yielding a measurable representation of the stored memory representations. Two recent studies using magnetic as well as sensory stimulation to the brain during VSTM maintenance provided proof of principle for the idea that pinging the system can yield a measurable code of an otherwise hidden stored representation (Rose et al., 2016; Wolff et al., 2017). Future studies are necessary to determine whether the observed attentional modulations of the SSVEP in chapter 3 and 4 reflect modulations of persistent memory-related sensory activity, or instead reflect measurable responses to a ping that reveal hidden memory states that otherwise remain beyond the detection threshold of non-invasive techniques. More generally, future studies should also determine the importance, if any, of short-term synaptic plasticity in VSTM, and test how such activity-silent synaptic mechanisms may functionally relate to persistent activity during VSTM.

The role of alpha-band activity in attention and VSTM

Representation-specific attentional modulations thus showed to be one important way in which attention influences VSTM. In chapter 2, I investigated whether distractor suppression during VSTM also relies on top-down modulation of alpha activity. Alpha oscillations have been proposed to form a powerful mechanism involved in the suppression of task-irrelevant processing, where increased alpha power has been shown to result in impaired sensory processing in task-irrelevant cortical regions (Frey, Ruhnau, & Weisz, 2015; Jensen & Mazaheri, 2010). Furthermore, the intrinsic waxing and waning of alpha power across oscillatory cycles has been proposed to reflect a mechanism of pulsed inhibition of neural processing (Bonnefond & Jensen, 2015; Mathewson et al., 2011; Samaha, Bauer, Cimaroli, & Postle, 2015), such that information processing is rhythmically inhibited at high-power phases of the alpha cycle, preventing information overload in downstream areas by temporarily inhibiting sensory processing. Importantly, alpha power in sensory cortex has been shown to be under top-down control (Marshall et al., 2015).

Results of the study presented in chapter 2 revealed the involvement of alpha activity during proactive, but not reactive distractor filtering during VSTM. Specifically, during VSTM of a stimulus display in which one hemifield was irrelevant as indicated by an attentional cue, we observed strong lateralization of occipital alpha power in anticipation of the memory display that was attenuated upon presentation of the memorandum, and returned again during maintenance in anticipation of the probe. Furthermore, we observed no alpha power modulations during reactive distractor filtering, when the precise number and spatial location of distractors was unpredictable. These results speak to two outstanding and puzzling questions concerning the role of alpha power oscillations in top-down modulation of neural processing. First, although the inhibitory function of alpha power modulations is now widely accepted (Jensen & Mazaheri, 2010; Payne & Sekuler, 2014), present knowledge on the extent to which the inhibitory function of alpha power in task-irrelevant sensory regions generalizes to VSTM is still limited. Secondly, it is still unclear whether alpha power modulations are predominantly involved in biasing of sensory processing across spatially separated cortical areas, or may also function at a more local scale or on a representation-specific basis (de Pesters et al., 2016; Sadaghiani & Kleinschmidt, 2016).

Research has only recently begun to address the first question of whether alpha-band oscillations can serve as a mechanism for top-down modulation of sensory processing to prevent storage of information in task-irrelevant regions, and thereby suppress distraction, during VSTM. Providing support for this notion, a seminal study showed that the strength of alpha activity scaled with the number of distractors presented in the task-irrelevant visual hemifield (Sauseng et al., 2009). Yet, we could not replicate this finding in chapter 2. We are also not aware of any other studies that could reproduce these findings. This calls into question to what extent alpha oscillations are associated with the suppression of storage of irrelevant information in VSTM, or instead serve as mechanism to prevent anticipated distraction in a load- or representation-unspecific manner. In two recent studies on alpha power modulations during VSTM, alpha power modulations after a precue were shown to reflect anticipatory attention, whereas alpha power modulations during VSTM maintenance after a retrocue were hypothesized to reflect controlled access to stored information in a spatially specific way (Kuo, Nobre, Scerif, & Astle, 2016; Myers, Walther, Wallis, Stokes, & Nobre, 2015). Together with the findings presented in chapter 2, these findings suggest that alpha activity may reflect the effects of directing attention to optimize VSTM performance, but not necessarily reflects suppression of stored representations. Furthermore, whereas the scalp topography of alpha activity during VSTM maintenance has been demonstrated to reveal the content of VSTM (Foster et al., 2016), this phenomenon may not be specific to VSTM, and may similarly occur during spatial attention (Samaha, Sprague, & Postle, 2016). Thus, at this point, convincing evidence for a role of alpha power modulations in distractor suppression during VSTM maintenance is lacking. Instead, alpha oscillations seem to facilitate attentional deployment to the task-relevant external as well as internal representations, in order to optimize optimal VSTM performance (Foster et al., 2016; Horschig, Jensen, van Schouwenburg, Cools, & Bonnefond, 2014).

A related outstanding question concerns the involvement of alpha oscillations in local and/or representation-specific versus spatially broad, regional modulation of sensory processing. This question is particularly hard to tackle in empirical research, especially when using scalp-level EEG recordings that are inherently characterized by a poor spatial resolution. In chapter 2, we tried to circumvent this limitation of scalp EEG by looking at aggregate alpha power measured across a set of lateral-occipital channels, and reasoned that any local changes in alpha power activity should be picked up by this set of occipital channels and should affect average alpha activity measured across these channels. Yet, we failed to observe evidence for such local modulations in the average activity levels across channels. The lack of evidence for distractor load-dependent changes in aggregate alpha power at lateral occipital sites in chapter 2 could indicate that alpha power is not involved in representation-specific suppression of representations stored in VSTM, but instead primarily gates sensory processing between task-relevant and irrelevant regions in a more general fashion. One possible pitfall, however, is that the inter-mixed presentation of trials requiring proactive as well as reactive filtering may have led to the adoption of a more generic filtering strategy across trials that prevented us from observing distractor-dependent modulations of alpha activity during VSTM (Jost & Mayr, 2016; Marini, Demeter, Roberts, Chelazzi, & Woldorff, 2016). Alternatively, aggregate alpha power across occipital channels may not be sensitive enough to the presence of such local alpha power modulations. Possibly, the detection of subtle and highly local modulations of alpha activity requires local measurements of neural activity. Indeed, recent findings from electrocorticography (ECoG) studies in humans support the notion that alpha oscillations not only subserve interregional biasing of information processing, but are also involved in the modulation of processing at a much finer spatial scale, and differentially affect processing of activity within a sensory region according to behavioral relevance (de Pesters et al., 2016; Harvey et al., 2013). Furthermore, fluctuations in the strength of local alpha activity measured in intralaminar recordings from primate visual cortex show evidence for a relationship between alpha activity and sensory processing, as measured in a relationship between the phase of alpha activity, and gamma power fluctuations or spiking responses (Dougherty, Cox, Ninomiya, Leopold, & Maier, 2015; Spaak et al., 2012). Interestingly, whereas the human studies indicate a role of alpha *power* in local modulations of sensory processing, this primate work instead suggests that alpha *phase* is essential for coordination of sensory processing at a local scale. Future research should examine to what extent alpha oscillations play a role in local modulations of sensory processing within cortical regions, and in particular the extent to which these modulations depend of alpha power and/or phase (Jensen, Gips, Bergmann, & Bonnefond, 2014).

Attentional filtering through differential modulation of relevant and irrelevant representations

Another unresolved question concerns whether attentional filtering improves goal-directed behavior by means of enhancement of goal-relevant information processing, suppression of goal-irrelevant information processing, or both. This question has been difficult to address in behavioral research, because both mechanisms presumably lead to reduced interference effects on behavioral performance (Adam & Vogel, 2016). Insights into the neural principles involved in selective attention are therefore critical for revealing the relative importance of enhancement and suppression in selective attention. Results from chapter 4 showed that during VSTM, differential modulation of target and distractor representations predicted VSTM performance, while attention to targets or distractors alone did not. This finding suggests that accurate memory performance in the presence of distraction depends on biasing competition between representations that may otherwise compete for the limited available storage space in VSTM (Desimone & Duncan, 1995; Franconeri, Alvarez, & Cavanagh, 2013; Shapiro & Miller, 2011).

Corroborating the notion that competition may underlie distractor-related interference effects and extending this finding to response selection, in chapter 5 we found that during a Simon task in which a task-irrelevant visual feature was associated with an incorrect response on a proportion of trials, performance across dimensions was negatively correlated across individuals. Concretely, while some individuals suffered more from interference by task-irrelevant motion direction, other individuals experienced more interference from task-irrelevant stimulus color. The feature-specific differences in susceptibility to distraction may indicate that the relative balance in information processing between competing task-relevant and task-irrelevant information may determine response conflict.

These findings may thus suggest that simultaneous modulation of relevant and irrelevant information processing, or the relative balance between two competing dimensions, determines distractor interference. Yet, recent studies have related efficient performance to distractor suppression per se. For example, individuals with low working memory capacity showed selective enhancement of task-relevant processing, whereas high working memory capacity individuals selectively suppressed distractors (Gaspar et al., 2016; Gulbinaite, Johnson, de Jong, Morey, & van Rijn, 2014). One possible discrepancy between these findings and our finding is that we assessed interference caused by different visual dimensions, whereas these earlier studies only assessed filtering of one type of interference. For example, it is possible that high and low working memory capacity (WMC) individuals would have exhibited different attentional strategies for different forms of visual interference, but this cannot be inferred from these earlier studies. In the context of VSTM, distractor suppression during VSTM maintenance was observed for temporally segregated information (Bonnefond & Jensen, 2012; Sreenivasan & Jha, 2007), but not for simultaneously presented information. Thus, contrary to the pattern emerging from these studies, results from the research described in chapter 2, 4 and 5 of this thesis jointly seem to indicate biased competition as the primary phenomenon underlying distractor filtering in service of performance.

In the present thesis, I interpreted the observed attentional modulations during VSTM performance in light of the idea that selective attention forms a bottleneck to VSTM, and thus determines the quality of VSTM (Awh & Vogel, 2008). Yet, there may well be a bidirectional relationship between VSTM and selective attention (Gazzaley, 2011): Ample evidence shows that the contents of VSTM also guide attentional selection of perceptual input (Olivers, 2008). As all findings reported in this thesis were correlational in nature, we cannot infer causal links between attention and VSTM. Although recent studies have shown that improved attentional filtering abilities following cognitive training lead to improved VSTM performance (Li, He, Wang, Hu, & Guo, 2017; Schmicker, Schwefel, Vellage, & Müller, 2016), supporting the deterministic role of selective attention in determining the quality of VSTM (as we presumed here), additional research is necessary to increase our understanding of how selective attention and VSTM may interact bidirectionally. Nevertheless, the presented findings support the notion of VSTM and attention as two strongly interdependent cognitive processes, that are closely linked in terms of their function as well as the neural mechanisms involved.

Does attention also contribute to VSTM performance during postperceptual stages?

Next to the question concerning the presence and role of sensory modulations during VSTM and response selection, a second important question in the present thesis concerned whether, and, how, attention helps protecting the contents of VSTM during postperceptual stages of VSTM following initial encoding.

Attention continues to support VSTM during VSTM maintenance

Results from chapter 3 and 4 of this thesis revealed the presence of ongoing attentional modulations during VSTM maintenance, and their importance for accurate VTSM performance. Thus far, the potential involvement of attention during VSTM maintenance was predominantly inferred from studies using retrocues. Retrocues are explicit attentional cues presented during VSTM maintenance that inform the participant which of the stored items will be relevant in a given trial, and which of the stored items are now irrelevant for the immediate behavioral goal, and can temporarily be set aside or even dropped from memory. Retrocues typically improve memory performance (Sligte, Scholte, & Lamme, 2008; Souza, Rerko, & Oberauer, 2015), which has been interpreted as evidence for the importance of selective attention even during postperceptual stages such as VSTM maintenance. Retrocues are particularly useful for studying how a specific memory item is prioritized by attention to guide subsequent behavior (Myers et al., 2017; Olivers, Peters, Houtkamp, & Roelfsema, 2011). Yet, they may not lend themselves well for studying the role and dynamics of sustained attention to internal representations in VSTM in situations in which all to-be-memorized items are equally important at a given time. The findings from chapters 3 and 4 corroborate previous findings from retrocueing studies by showing that attention is involved in keeping information active in VSTM, and extend these findings by showing that this occurs even in the absence of explicit instructions to prioritize a single stored item for behavioral use. Attention thus appears to be important for active maintenance of information in VSTM.

Temporal dynamics of attention reveal mechanism of sequential rehearsal

The persistent attentional modulation of stored representations during VSTM maintenance observed in chapter 3 might play a role in rehearsal of the stored representations, in order to keep these representations active in VSTM. According to the prominent attention-based rehearsal account of VSTM (Awh, Jonides, & Reuter-Lorenz, 1998), the deployment of spatial attention across stored locations during VSTM may serve to keep stored representations in VSTM in an active and accessible state. Yet, this account is not explicit about the temporal dynamics of spatial rehearsal during VSTM. Inspired by intriguing findings showing rhythmic attentional sampling during perception (Dugué, McLelland, Lajous, & VanRullen, 2015; Fiebelkorn, Saalmann, & Kastner, 2013; Landau & Fries, 2012), in chapter 3, we hypothesized that spatial attention may also rehearse or sample stimulus representations in a sequential or rhythmic fashion during VSTM.

Indeed, preliminary results from exploratory cross-correlation analyses in chapter 3 were indicative of sequential attentional rehearsal of individual stimulus representations during VSTM maintenance. This finding suggests that there may be fluctuations in the extent to which internal representations are in the focus of attention, in line with a recent proposal of rhythmic attentional rehearsal during VSTM by means of top-down reactivation of (high frequency) sensory activity associated with stored representations (Van Vugt, Chakravarthi, & Lachaux, 2014). Another recent intracranial EEG study on the role of hippocampal oscillations in reactivation of stored representations during working memory also provides evidence for rhythmic VSTM reactivation. In this study, periods of memory reactivation were locked to hippocampal delta oscillations (Leszczynki, Fell, & Axmacher, 2015). These periods of hippocampal memory reactivation were accompanied by enhanced neuronal excitability in regions involved in processing of the stored stimulus, as reflected in decreased region-specific alpha activity. Interestingly, the observed hippocampal delta oscillations fall into a comparably slow range as the lagged correlations observed in chapter 3 of this thesis. Conceivably, and speculatively, but in line with its alleged role in the encoding of experience, the hippocampus may be driving the cortical reactivation of memory representations during VSTM.

The notion of sequential rather than simultaneous activation of short-term memory representations is also relevant in light of the idea of that only a single item in VSTM can be in the focus of attention and guide perceptual selection and behavior, the so-called attentional template (Olivers et al., 2011). Reconciling the notion that only one item in VSTM can be in the focus of attention and the idea of sequential rehearsal during VSTM, it is possible that the attentional template or focus of attention is not consistently occupied by a single representation, but instead alternates between different stored representations in a rhythmic or sequential fashion. A recent modeling study using the framework of synaptic-based working memory to model simultaneous maintenance of multiple representations in VSTM showed that such sequential activations during VSTM may be a biophysically plausible mechanism underlying maintenance of multiple items in VSTM (Mi, Katkov, & Tsodyks, 2017). Future research is necessary to replicate and determine whether the observed sequential activation of representations in chapter 3 concerns the sequential alternation of the representation occupying the attentional template.

The importance of an individual differences approach in cognitive neuroscience research

The notion that individual differences in cognitive performance provide an interesting source of variance is gradually replacing the long prevailing view that differences in performance across individuals reflect noise (Vogel & Awh, 2008; Zilles & Amunts, 2013). In the present thesis, we exploited individual differences in the ability to filter distraction during VSTM and response selection in order to identify and validate neural markers of optimal attentional performance. Corroborating previous research, in chapters 2 and 4, we found that the ability to filter task-irrelevant information predicted individual VSTM performance in the presence of distraction, as reflected in the degree to which distractors were prevented from being needlessly stored in VSTM (chapter 2), and differential attentional deployment to targets and distractor representations (chapter 4). In chapter 3, we found that individual differences in attentional deployment to relevant locations during encoding of information predicted VSTM performance across individuals. In addition, the degree to which task-irrelevant information from different visual dimensions induced response conflict in chapter 5 differed across individuals. While some individuals showed strong interference by task-irrelevant motion direction, but were less susceptible to interference by stimulus color, other individuals showed the opposite pattern. These individual differences in susceptibility to task-irrelevant distractors in turn predicted individual differences in conflict-related theta activity. Thus, individual differences analyses confirmed the important role of attentional modulation of sensory activity in goal-directed behavior, and illustrate the usefulness of an individual differences approach in understanding the relationship between neurophysiological measures and behavior.

In chapter 4 and 5, individual differences analyses also revealed the presence of multiple attentional dynamics or strategies, which could not be derived from the pattern observed at the group level. In chapter 4, some individuals suffered more from a low distractor load with uniformly colored distractors, whereas other suffered more from a high distractor load with differently colored distractors. Yet, at the group level, distractor load did not affect VSTM performance or attentional deployment. Similarly, in chapter 5, some individuals suffered more from interference by task-irrelevant stimulus color, whereas others suffered more from interference by task-irrelevant motion direction of the stimulus. This result corroborates findings from earlier EEG studies that dissociated 'color-suppressors' from 'motion-suppressors' (Snyder & Foxe, 2010) or 'global-feature-suppressors' from 'local-feature-suppressors' (Ridderinkhof & van der Molen, 1995). Again, the pattern emerging from the individual-differences analyses revealed entirely different dynamics than the group-level results alone: The group level results suggested that motion direction and stimulus color induced comparable conflict effects when being irrelevant to the task at hand, which were both associated with a mid-frontal theta response that was independent of the size of the experienced conflict. Yet, individual differences analyses revealed that the strength of the mid-frontal theta response was in fact dependent of the size of the conflict effect, but only when taking individual differences in sensitivity to different visual dimensions into account. These observations exemplify how taking an individual differences perspective can reveal essential dynamics that remain hidden when studying group averaged data only.

Future Directions

The findings presented in this thesis have provided important insights into the role of attention for VSTM and goal-directed behavior, but at the same time also raise questions that need further attention in future research. I will outline some important directions for future research below.

First, the work presented in this thesis concerned neurotypical and young adults. It will be important to extend this work to clinical populations that suffer from attention and/or VSTM problems. People with ADHD, for example, have problems with sustained focusing of attention, and also suffer from problems with goal-directed response selection. There is evidence showing that neuronal mechanisms that critically support selective attention, such as the ability to modulate occipital alpha activity, is impaired in children and adults with ADHD (ter Huurne et al., 2013; Vollebregt, Zumer, Huurne, Jensen, & Buitelaar, 2003). Furthermore, individuals with ASD tend to display an impaired ability to control sensory information processing (Booth & Happé, 2016; Keehn, Müller, & Townsend, 2013). Yet, the extent to which these problems generalize to attentional control in the context of VSTM or response selection is still largely unknown and forms an important direction for future research.

Another key question for future research concerns how attentional filtering during VSTM and response selection is affected by age. Various studies have now shown evidence for the notion that attentional filtering abilities are affected by age (Kerstin Jost, Bryck, Vogel, & Mayr, 2011; McNab et al., 2015; Schwarzkopp, Mayr, & Jost, 2016), and unpublished work from our lab suggests that this deterioration may already start at around the age of 40. Furthermore, alpha power modulations during VSTM may be diminished in healthy older adults (Leenders, Lozano-Soldevilla, Roberts, Jensen, & De Weerd, 2016), while alpha modulations in response to retrocues during VSTM may still be preserved with age (Mok, Myers, Wallis, & Nobre, 2016). The precise developmental trajectory of attentional filtering, and the neural mechanisms involved herein, thus also provides an important direction for future research. More generally, clinical or elderly populations may exhibit an even more diverse range of behavioral and neural variability than the typical population, forming a valuable source of information to study the functional role of the neural mechanisms involved.

Although future studies in aging and atypical populations are important to reveal the neural mechanisms underlying functional impairments of selective attention or VSTM, knowledge about what goes wrong in the atypical brain may not necessarily advance understanding of how the healthy brain realizes complex cognitive functions such as the temporary storage of representations to control behavior. In order to significantly further our knowledge on the role of selective attention in VSTM and goal-directed behavior, an important direction for future research seems to focus on the fundamental mechanisms, or neural codes, used to represent information stored in VSTM or guiding goal-directed behavior, and the way attention may operate on these codes. Specifically, as described earlier in this Discussion section, the results from chapter 3 and 4 of this thesis, as well as a large body of earlier work (Emrich, Riggall, Larocque, & Postle, 2013; Serences et al., 2009), suggest that representations during VSTM could be sensory in nature. Yet, increasingly popular accounts of dynamic and distributed coding posit that during VSTM, representations are stored in hidden patterns of synaptic weights or functional connectivity (Mi et al., 2017; Stokes, 2015), or in distributed patterns of cortical activity (Christophel et al., 2017). Presently, the existence of hidden states is typically inferred from findings showing that temporarily task-irrelevant items in VSTM are not accompanied by detectable activity patterns representing this irrelevant item, while a change in task demands rendering the item of interest goal-relevant again, converts the item into a measurable representation in the brain (Wolff et al., 2017). From such findings, it appears as if the identity of the item of interest was continuously present, but initially stored in a hidden configuration. Yet, actual evidence for the presence and neural format of hidden states is presently still limited. In the context of the notion of distributed codes, the mechanism by which distributed patches of neurons may form coherent representations, needs further attention in future research (Christophel et al., 2017). Insights into the precise neural codes used to temporarily store information and flexibly guide behavior will significantly advance the field (Myers et al., 2017; Zelinsky & Bisley, 2015). Specifically, adopting a systems-level approach to reveal potentially hidden or distributed representations at local as well as interregional levels, for example by studying and linking codes reflected in modulations of synaptic weights, distributed activity patterns, as well interregional phase synchronization, seems an important direction for future research that will advance our understanding of the neural mechanisms underlying the ability to perform goal-directed actions in everyday life.

Conclusion

The research described in this thesis reveals key insights into how attentional filtering may contribute to effective VSTM performance and response selection, and the importance of individual differences analyses to obtain insights into these phenomena. One pivotal way in which attention supports VSTM and response selection is by means of continuous modulations of sensory processing. Another important pattern emerging from the reported research is that people differ strongly in the extent to which they are distracted by different forms of visual interference: What may be distracting to you, may not affect your friend's concentration or ability to complete an intended action. Thus, while interference conceivably results from needlessly intensive processing of the distracting information, the degree to which individuals are distracted by task-irrelevant information in daily life is at least in part specific to the source of interference.

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Chapter 2

M.E.V. and H.A.S. designed the study. Data collection was performed by M.E.V. M.E.V. performed the data analysis and interpretation in consultation with J.v.D. and H.A.S. M.E.V. drafted the manuscript and J.v.D. and H.A.S. provided critical revisions. This study was supported by a VIDI Grant from the Netherlands Organisation for Scientific Research (NWO), awarded to H.A. Slagter.

Chapter 3

M.E.V., R.G., and H.A.S. designed the study. Data collection was performed by B.P.B. and M.E.V. M.E.V. performed the data analysis and interpretation in consultation with R.G., R.P.P.P.G., and H.A.S. M.E.V. drafted the manuscript and B.P.B., R.G., R.P.P.P.G., and H.A.S. provided critical revisions. This study was supported by a VIDI Grant from the Netherlands Organisation for Scientific Research (NWO), awarded to H.A. Slagter.

Chapter 4

M.E.V., R.G., and H.A.S. designed the study. Data collection was performed by T. v.d. B. and M.E.V. M.E.V. performed the data analysis and interpretation in consultation with R.G. and H.A.S. M.E.V. drafted the manuscript and T. v.d. B., R.G., and H.A.S. provided critical revisions. This study was supported by a VIDI Grant from the Netherlands Organisation for Scientific Research (NWO), awarded to H.A. Slagter.

Chapter 5

M.E.V. and M.X.C. designed the study. Data collection was performed by M.E.V. M.E.V. performed the data analysis and interpretation in consultation with K.R.R., H.A.S, and M.X.C. All authors contributed to the manuscript.

LIST OF PUBLICATIONS

Research presented in this thesis

Chapter 2

Vissers, M.E., van Driel, J., & Slagter, H.A. (2016). Proactive, but Not Reactive, Distractor Filtering Relies on Local Modulation of Alpha Oscillatory Activity. *Journal of Cognitive Neuroscience, 28*(12), 1964–1979.

Chapter 3

Vissers, M.E., Gulbinaite, R., Grasman, P.P.P., Bramson, B.P., & Slagter, H.A. Spatiotemporal dynamics of attention during visual short-term memory. Manuscript under review.

Chapter 4

Vissers, M.E., Gulbinaite, R., van den Bos, T., & Slagter, H.A. (2017). Protecting visual short-term memory during maintenance: Attentional modulation of target and distractor representations. *Scientific Reports, 7*(1), 4061.

Chapter 5

Vissers, M.E., Ridderinkhof, K.R., Cohen, M.X*, & Slagter, H.A.* Oscillatory mechanisms of response conflict elicited by color and motion direction: an individual differences approach. Submitted manuscript. *Shared senior authorship.

Other Publications

Jensen, O., & Vissers, M.E. Multiple visual objects are sampled sequentially. *PLoS Biology, 15(7)*, e2003230.

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NEDERLANDSE SAMENVATTING

Selectieve aandacht en het kortetermijngeheugen zijn van fundamenteel belang om goed te kunnen functioneren in het dagelijks leven. De hoeveelheid sensorische informatie die voortdurend op ons af komt is groot en bevat vaak een overdaad aan details. Onze hersenen hebben echter maar een beperkte capaciteit. Hierdoor kan niet alle informatie uit de omgeving tegelijkertijd worden verwerkt, opgeslagen of gebruikt voor het aansturen van gedrag. Zelfs tijdens een ogenschijnlijk eenvoudige alledaagse handeling, zoals het oversteken van een straat, is het belangrijk om de waargenomen informatie te kunnen filteren, om zo alleen relevante informatie te verwerken en vervolgens op te slaan in het geheugen. Bij het oversteken gebeurt er van alles tegelijk: er komen taxi's en fietsers op je af, er steken mensen over, er komt een tram langs die stilhoudt en in je ooghoek zie je een horde toeristen uit een bus stappen. Als je niet in staat bent om alleen op de informatie te letten die belangrijk is om veilig te kunnen oversteken, of als je deze informatie niet kunt onthouden zodat je kunt plannen wanneer en hoe je over zal steken, lukt het je waarschijnlijk niet om zonder ongelukken de overkant van de straat te bereiken.

De rol van aandacht en kortetermijngeheugen in doelgericht gedrag

Selectieve aandacht stelt ons in staat om specifiek die informatie uit onze omgeving te verwerken die relevant is voor doelmatig handelen. Het opslaan van informatie gebeurt in het kortetermijngeheugen, waarin maar een beperkte hoeveelheid informatie tijdelijk kan worden opgeslagen: we kunnen slechts een handvol representaties tegelijkertijd in een actieve staat bewaren en gebruiken voor het aansturen van gedrag (Cowan, 2001). Om overbelasting van deze beperkte capaciteit te voorkomen is het nodig om waargenomen informatie zoveel mogelijk te filteren op basis van de relevantie ervan voor gestelde doelen (Vogel, McCollough, & Machizawa, 2005). Selectieve aandacht omvat precies dit vermogen, en speelt daarmee een belangrijke rol in het bepalen van de inhoud van het kortetermijngeheugen en het realiseren van doelgericht gedrag.

Het belang van selectieve aandacht voor de efficiënte uitvoering van andere essentiële cognitieve processen, zoals het kortetermijngeheugen of het vermogen om doelgerichte handelingen te kunnen selecteren in de aanwezigheid van interferentie (responsselectie), wordt breed ondersteund in eerder gedragsonderzoek (Gazzaley & Nobre, 2012; Kane & Engle, 2003). In hersenonderzoek is daarnaast aangetoond dat fluctuaties in hersenactiviteit in zowel corticale als subcorticale hersengebieden, waaronder de prefrontale cortex en kernen in de basale ganglia, samenhangen met het succesvol voorkomen of onderdrukken van afleidende informatie (Baier et al., 2010; McNab & Klingberg, 2008). In de context van kortetermijngeheugen worden deze gebieden vaak beschouwd als poortwachters, die informatie filteren zodat alleen doelrelevante informatie wordt doorgelaten en opgeslagen in het kortetermijngeheugen (Awh & Vogel, 2008). In de context van responsselectie worden deze gebieden verondersteld betrokken te zijn bij het monitoren en controleren van activatie van verschillende responstendensen, zodat eventuele handelingen die niet bijdragen aan een voorgenomen doel, kunnen worden afgeremd voordat ze werkelijk zijn uitgevoerd (Carter & van Veen, 2007; Ridderinkhof, Forstmann, Wylie, Burle, & van den Wildenberg, 2011). Dit eerdere onderzoek laat zien dat frontale en subcorticale controlemechanismen een belangrijke rol vervullen in het beschermen van cognitieve processen tegen afleiding tijdens kortetermijngeheugen en responsselectie. Echter, het is vooralsnog onduidelijk of selectieve aandacht en het voorkomen van afleiding in de context van kortetermijngeheugen of responsselectie mogelijk ook deels berusten op het aanpassen van de verwerking van sensorische informatie.

Doelrelevante en afleidende informatie zijn in eerste instantie voornamelijk sensorisch van aard. Het is dus niet ondenkbaar dat de beïnvloeding van sensorische verwerking van informatie direct effect heeft op efficiënt cognitief functioneren (Zelinsky & Bisley, 2015). Bovendien laat steeds meer onderzoek zien dat het aanpassen van de sensorische verwerking van waargenomen informatie een belangrijke rol speelt in het faciliteren van doelgericht gedrag, in contrast met eerdere opvattingen dat de beïnvloeding van neurale activiteit ten behoeve van doelgericht functioneren pas plaatsvindt na initiële sensorische verwerking van informatie (Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009). Het is echter nog grotendeels onduidelijk hoe het aanpassen van de sensorische verwerking van doelrelevante en irrelevante informatie bijdraagt aan processen zoals kortetermijngeheugen en responsselectie, vooral wanneer deze processen plaatsvinden in de aanwezigheid van een grote hoeveelheid informatie tegelijkertijd. Daarnaast is nog onduidelijk wat de temporele dynamiek is van aandachtsprocessen tijdens kortetermijngeheugen en responsselectie: is selectieve aandacht vooral belangrijk bij het inprenten van informatie uit de omgeving? Of blijft aandacht continu van belang, ook tijdens het vasthouden van informatie in het kortetermijngeheugen of het uitvoeren van een geplande handeling? Inzichten in de wijze waarop selectieve aandacht een effect heeft op sensorische informatieverwerking om zo afleiding te minimaliseren in de context van kortetermijngeheugen en responsselectie zijn essentieel voor een beter begrip van de manier waarop selectieve aandacht kan bijdragen aan efficiënt en doelgericht gedrag.

Doel van dit proefschrift

Op dit moment weten we nog maar weinig over hoe en wanneer precies in de tijd selectieve aandacht bijdraagt aan de effectiviteit van ons kortetermijngeheugen en responsselectie, en of dit gebeurt middels de modulatie van sensorische activiteit. De centrale vraag in dit proefschrift betrof daarom de manier waarop selectieve aandacht bijdraagt aan efficiënte opslag van informatie in het kortetermijngeheugen en doelgericht gedrag. Ik was specifiek geïnteresseerd in de mogelijkheid dat deze mechanismen berusten op de beïnvloeding van de sensorische verwerking en representatie van waargenomen informatie, om zo doelgericht gedrag te faciliteren. Deze mogelijkheid werd onderzocht door de neurale mechanismen die betrokken zijn bij selectieve aandacht te bestuderen. Inzichten in deze neurale mechanismen werden grotendeels verkregen door te onderzoeken of individuele verschillen in aandachtsprocessen tijdens kortetermijngeheugen of responsselectie konden worden verklaard door verschillen in de neurale mechanismen die we tijdens deze processen observeerden met behulp van EEG. EEG, het elektro-encefalogram, is een methode om elektrische stroompjes te kunnen meten die worden afgegeven door een deel van de neuronen in de cortex (de hersenschors). Wanneer de sterkte van een bepaalde neuraal effect (bijvoorbeeld een EEG signaal in taak-irrelevante gebieden) correleert met een bepaalde maat van doelgericht gedrag (bijvoorbeeld de mate waarin iemand afleiding kan negeren), dan geeft dit aanleiding om te veronderstellen dat het neurale effect geassocieerd is met een functioneel mechanisme dat betrokken is bij het selecteren van waargenomen informatie. In alle hoofdstukken van dit proefschrift werd het effect van selectieve aandacht op sensorische informatieverwerking onderzocht in het visuele domein, omdat het visuele systeem de meeste aanknopingspunten biedt om aandachtsprocessen te kunnen meten in het brein met behulp van EEG.

Een eerste openstaande vraag die ik heb onderzocht is hoe waargenomen informatie uit de omgeving verschillend wordt verwerkt en vastgehouden in het kortetermijngeheugen afhankelijk van de relevantie ervan voor een bepaald voorgenomen doel. Eerder onderzoek laat zien dat aandacht het mogelijk maakt de kortetermijngeheugencapaciteit optimaal te gebruiken door selectief doelrelevante informatie toe te laten in het geheugen (Gazzaley, 2011; Gazzaley & Nobre, 2012; Vogel et al., 2005). Echter, het is nog onduidelijk in hoeverre selectieve opslag van informatie berust op het aanpassen van de sensorische verwerking van relevante items, onderdrukking van irrelevante of afleidende stimuli, of beide mechanismen (Adam & Vogel, 2016).

De hierboven beschreven vraag gaat over *hoe* aandacht helpt om informatie op te slaan in het kortetermijngeheugen. Een tweede vraag die nog grotendeels onbeantwoord is gebleven is *wanneer* aandacht een rol speelt in het ondersteunen van opslag van doelrelevante informatie in het kortetermijngeheugen. Uit eerder onderzoek weten we dat selectieve aandacht nodig is om doelrelevante informatie goed in te kunnen prenten in het geheugen. De mate waarin aandacht ook van belang is om deze informatie actief te kunnen houden in het geheugen, is echter nog onduidelijk. Voorgaand onderzoek naar de rol van selectieve aandacht in het ondersteunen van het kortetermijngeheugen maakte voornamelijk gebruik van expliciete aandachts-instructies tijdens het retentie interval (Griffin & Nobre, 2003; Souza & Oberauer, 2016). Dit onderzoek liet onbeantwoord of aandacht een vergelijkbare rol vervult als er geen expliciete instructies worden gegeven tijdens kortetermijngeheugen. Daarnaast weten we niet of aandacht een proces is dat verschillende geheugenrepresentaties continu en tegelijkertijd versterkt, of dat aandacht een dynamischer proces is met een beperkte capaciteit, en bijvoorbeeld achtereenvolgend verschillende relevante representaties uitlicht (Van Vugt, Chakravarthi, & Lachaux, 2014). Een laatste vraag in dit proefschrift betrof de mate waarin verschillende typen van irrelevante visuele informatie kunnen leiden tot verschillende of vergelijkbare automatische activatie van incorrecte handelingen (Galashan, Wittfoth, Fehr, & Herrmann, 2008; Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012).

Het onderzoek en de resultaten

De eerste belangrijke vraag in dit proefschrift betrof de vraag of efficient gebruik van onze zeer beperkte kortetermijngeheugencapaciteit, berust op het aanpassen van de sensorische verwerking van waargenomen informatie afhankelijk van hoe belangrijk deze informatie is een voorgenomen doel. Dit idee wordt aangehangen in de recentelijk populairder wordende ‘sensorische rekruterings-theorie’ van kortetermijngeheugen (Ester, Serences, & Awh, 2009; Zelinsky & Bisley, 2015). Echter, huidig empirisch bewijs voor dit idee is beperkt en kan vaak niet worden gegeneraliseerd naar situaties die vergelijkbaar zijn met kortetermijngeheugen in het dagelijks leven, buiten het laboratorium. Voorgaand onderzoek toetste dit idee bijvoorbeeld alleen in situaties waarin mensen slechts een minimale hoeveelheid informatie hoefden te onthouden. Daarnaast werd in dit onderzoek niet bekeken of en hoe aanpassingen van sensorische activiteit tijdens VSTM in de aanwezigheid van afleidende informatie helpen om afleiding te minimaliseren. In hoofdstuk 2, 3 en 4 werd onderzocht of het inprenten en vasthouden van doelrelevante informatie in kortetermijngeheugen berust op aandachtmodulaties van activiteit in hersengebieden die betrokken zijn bij visuele verwerking van waargenomen informatie. Hierbij werd specifiek gekeken naar twee verschillende manieren waarop sensorische activiteit in deze gebieden kan worden gemoduleerd. Als eerste werd in hoofdstuk 2 onderzocht of modulatie van de sterkte van alfa golven in de occipitale cortex een rol speelt bij het voorkomen van en onderdrukken van afleiding tijdens kortetermijngeheugen. In hoofdstuk 3 en 4 werd onderzocht of modulatie van representatie-specifieke sensorische activiteit een rol speelt tijdens het opslaan en vasthouden van informatie in het kortetermijngeheugen.

Alfa golven in de hersenen hebben een frequentie van ongeveer 10 Hz en spelen een belangrijke rol in selectieve aandacht (Jensen & Mazaheri, 2010; Klimesch, 2012; Payne & Sekuler, 2014). Voorgaand onderzoek heeft aangetoond dat tijdens de waarneming van informatie die vergezeld wordt door irrelevante informatie die in een ander deel van de hersenen wordt verwerkt, de sterkte van alfa oscillaties afneemt in taak-relevante sensorische gebieden, terwijl de sterkte ervan tegelijkertijd toeneemt in taak-irrelevante sensorische gebieden. Op basis hiervan wordt verondersteld dat het reduceren van alfa activiteit inhibitie van neurale activiteit reduceert, en op deze manier een betere verwerking van informatie in dat deel van de cortex mogelijk maakt. Sterkere alfa activiteit daarentegen, wordt verondersteld te zorgen voor een hoge mate van inhibitie, en dus verminderde verwerking van informatie in het betreffende deel van de cortex. Op deze manier vormt de lokale modulatie van de sterkte van alfa golven in taak-relevante en taak-irrelevante hersengebieden een belangrijk mechanisme bij het voorkomen van afleiding tijdens perceptie. De mate waarin alfa golven ook een rol spelen bij het onderdrukken van afleiding tijdens kortetermijngeheugen is echter nog grotendeels onbekend.

In hoofdstuk 2 werd specifiek onderzocht of de modulatie van alfa golven in de visuele cortex een rol speelt tijdens proactieve en reactieve onderdrukking van verwachte en onverwachte afleiding, respectievelijk, bij het inprenten en vasthouden van informatie in het kortetermijngeheugen. Proefpersonen deden een kortetermijngeheugentaak waarin ze de opdracht kregen de kleur van kort gepresenteerde plaatjes met simpele figuren goed te onthouden. De informatie die moest worden onthouden, werd gepresenteerd in de aanwezigheid van een aantal afleiders in de vorm van andere figuren waarvan proefpersonen wisten dat ze irrelevant waren voor de geheugentaak. Door middel van de presentatie van een pijl naar de locatie waar de relevante figuren zouden verschijnen, konden de proefpersonen de presentatie van een aantal afleiders voorzien. Tegelijkertijd konden er daarnaast onverwacht afleiders worden gepresenteerd tussen de relevante figuren; een vorm van afleiding die veel minder voorspelbaar was. Na een kort interval waarin de figuren werden verwijderd van het scherm werden ze opnieuw getoond, alleen was in sommige gevallen een van de figuren van kleur veranderd. Het geheugen van de proefpersonen werd getoetst door te meten hoe goed proefpersonen in staat waren een verandering te detecteren in de kleur van de tweede ten opzichte van de eerste set figuren. De mate van afleiding werd gekwantificeerd door te meten hoe sterk geheugenprestaties achteruit gingen door de aanwezigheid van afleiding. Terwijl proefpersonen deze taak volbrachten werd hun hersenactiviteit gemeten met behulp van EEG. EEG is bijzonder geschikt om snelle veranderingen in hersenactiviteit te onderzoeken: EEG heeft vergeleken met een aantal ander prominente methoden om hersenactiviteit te onderzoeken, zoals fMRI, een hoge temporele resolutie. Een belangrijke beperking van EEG is echter dat de hersenactiviteit wordt gemeten op het niveau van de schedel, waardoor het signaal dat wordt gemeten is verstoord door de hersenvloeistof en de schedel, voor het uiteindelijk door de sensoren wordt opgepikt. Deze verstoringen maken het vooral moeilijk om te bepalen waar precies in het brein activiteit wordt gegenereerd, maar hebben gelukkig nagenoeg geen effect op de temporele fluctuaties van het gemeten signaal. In dit proefschrift gebruikten we EEG om de temporele karakteristieken van het effect van aandacht op neurale activiteit te bestuderen, zonder specifiek te onderzoeken waar in het brein deze activiteit vandaan komt.

Resultaten van het EEG-onderzoek in hoofdstuk 2 lieten zien dat de sterkte van alfa golven gemeten boven een taak-irrelevant gebied van de cortex een rol speelden in anticipatie op verwachte afleiding: voorafgaand aan de presentatie van de plaatjes nam de sterkte van de alfa activiteit toe gemeten boven taak-irrelevante visuele schedelgebieden (het achterhoofd), en nam tegelijkertijd de sterkte van de alfa golven af gemeten boven taak-relevante visuele schedelgebieden. Daarnaast hadden de verwachte afleiders geen effect op geheugenprestaties: geheugenprestaties varieerden niet als functie van de hoeveelheid verwachte afleiding. Mogelijk helpen alfa golven om afleiding door verwachte irrelevante informatie te voorkomen door middel van lokale inhibitie van sensorische verwerking (Jensen & Mazaheri, 2010). Een alternatieve mogelijkheid is dat de gevonden modulatie van alfa golven de rekrutering van ander onderliggend mechanisme reflecteert dat helpt om afleiding te voorkomen en tegelijkertijd gepaard gaan met modulatie van alfa golven in sensorische gebieden. In het geval van afleiding die niet precies kon worden voorspeld, speelde modulatie van alfa activiteit geen rol. Echter, de gedragsresultaten en resultaten van ‘event-related potential’ (ERP) analyses van de EEG data uit dit onderzoek lieten zien dat de proefpersonen wel degelijk in staat waren om in ieder geval deels te voorkomen dat deze onverwachte afleiders werden opgeslagen in het kortetermijngeheugen. ERP’s reflecteren de gemiddelde fluctuatie in hersenactiviteit gemeten op een bepaald schedelgebied, als gevolg van een bepaalde gebeurtenis (in ons geval, de presentatie van een geheugenscherm met of zonder afleiders). De amplitude van een ERP component die geassocieerd is met het initieren van het filteren van onverwachte afleiding tijdens kortetermijngeheugen (Liesefeld, Liesefeld, & Zimmer, 2014), varieerde ook in hoofdstuk 2 afhankelijk van de aanwezigheid van onverwachte afleiding. Bovendien was het effect van onverwachte afleiders op de amplitude van deze ERP component voorspellend voor de mate waarin deze afleiders onnodig werden opgeslagen in het kortetermijngeheugen, gemeten middels de amplitude van een ERP component die indiceert hoeveel informatie er is opgeslagen in het kortetermijngeheugen. Deze bevindingen geven aan dat het gebrek aan bewijs voor een rol voor alfa activiteit in het filteren van onverwachte afleiding in hoofdstuk 2, niet simpelweg kan worden verklaard doordat proefpersonen niet filterden.

Het onderzoek uit hoofdstuk 2 toont aan dat modulatie van de sterkte van alfa golven in taak-relevante en taak-irrelevante gebieden selectief een rol speelt bij het voorkomen van verwachte afleiding. In het dagelijks leven kunnen we echter niet altijd voorspellen waar en wanneer er afleiding komt, en lijken we desondanks, in ieder geval tot op zekere hoogte, te kunnen voorkomen dat we door deze afleiding ons doel niet meer kunnen bereiken. Dit bleek ook uit de resultaten van de ERP analyses in hoofdstuk 2. Echter, de resultaten uit dit hoofdstuk boden geen ondersteuning voor de mogelijkheid dat de modulatie van alfa activiteit tijdens kortetermijngeheugen een mechanisme vormt waarmee sensorische verwerking kan worden beïnvloed om onverwachte afleiding te filteren.

In hoofdstuk 3 en 4 van dit proefschrift werd onderzocht of modulatie van representatie-specifieke sensorische verwerking tijdens het inprenten en vasthouden van informatie in het kortetermijngeheugen voorspelt hoe goed informatie is onthouden, en hoe goed onverwachte afleiding kan worden onderdrukt. Deze vraag is relevant in het licht van eerder onderzoek waaruit blijkt dat de mate waarin mensen selectief doelrelevante informatie in hun geheugen kunnen opslaan, voorspelt hoe groot hun geheugencapaciteit is (Luck & Vogel, 2013). Tot nu toe weten we echter nog niet goed hoe de selectieve opslag van informatie in het kortetermijngeheugen precies plaatsvindt. Eerder onderzoek naar de rol van selectieve aandacht bij het vasthouden van informatie in het kortetermijngeheugen (Souza & Oberauer, 2016), maakte gebruik van aandachts-instructies die niet noodzakelijkerwijs inherent zijn aan meer typische situaties waarin je iets probeert te onthouden, en waarin je geen aanwijzingen krijgt voor het richten van je aandacht. Om aandacht tijdens kortetermijngeheugen te kunnen volgen zonder expliciete instructies te gebruiken, maakte ik in hoofdstuk 3 en 4 gebruik van zogenaamde steady-state evoked potentials (SSVEP’s). SSVEP’s zijn neurale responsen die kunnen worden gemeten met EEG tijdens ritmische stimulering van het sensorische, in ons geval visuele systeem. Ritmische contrastveranderingen van een stimulus resulteren in een neurale respons in visuele gebieden van de cortex (Norcia, Appelbaum, Ales, Cottereau, & Rossion, 2015). Deze respons heeft bovendien exact dezelfde frequentie als de frequentie waarmee de stimulus van contrast verandert. Dit principe is bijzonder nuttig in onderzoek naar aandacht, omdat aandacht sensorische responsen (zoals SSVEP's) versterkt (Muller, Bartelt, Donner, Villringer, & Brandt, 2003). Door het gebruik van verschillende frequenties voor SSVEP's die worden geïnduceerd op verschillende locaties op het scherm, kan de verdeling van aandacht over meerdere individuele locaties tegelijkertijd worden gevolgd aan de hand van de unieke 'frequentie-labels' voor de verschillende locaties. Bovendien kan met behulp van SSVEP's aandachtsturing worden gevolgd in de tijd, zodat temporele kenmerken van aandachtsverdeling tijdens het inprenten en vasthouden van informatie in het kortetermijngeheugen kunnen worden onderzocht. Het gebruik van SSVEP's in hoofdstuk 3 en 4 maakte het mogelijk om de verdeling van aandacht over verschillende objecten tegelijkertijd te kunnen volgen, zonder dat aandacht werd gemanipuleerd met behulp van expliciete instructies. Daarnaast maakte deze benadering het mogelijk om te onderzoeken of aandacht alleen een rol speelt bij het inprenten van informatie in kortetermijngeheugen, of dat aandacht ook belangrijk is voor het actief houden van deze informatie in het kortetermijngeheugen.

Zowel hoofdstuk 3 als 4 leverden ondersteuning voor de notie dat aandacht ook tijdens het vasthouden van informatie in het kortetermijngeheugen nog een belangrijke rol speelt: de modulaties van geheugenrepresentaties duurden voort tijdens het retentie interval van de geheugentaak. Deze inzichten zijn vernieuwend, omdat ze laten zien dat de rekrutering van aandacht tijdens kortetermijngeheugen niet afhangt van een expliciete instructie om aandacht te gebruiken, maar ook plaatsvindt in de afwezigheid van zulke instructies. De rol van aandacht werd afgeleid uit de geobserveerde aanpassingen van modulaties van de SSVEP's. Aandacht beïnvloedt kortetermijngeheugen dus in elk geval deels door het aanpassen van de sensorische verwerking van relevante en irrelevante representaties. De geobserveerde modulaties tijdens het vasthouden van informatie in het kortetermijngeheugen in aanwezigheid van afleiding hadden een belangrijke functionele rol: hoe sterker deze modulaties, hoe beter mensen doelrelevante informatie konden opslaan in hun geheugen. Resultaten van hoofdstuk 4 toonden bovendien aan dat het onderdrukken van afleiding tijdens kortetermijngeheugen berust op differentiatie van aandacht naar relevante en irrelevante representaties. Individuele verschillen in de sterkte van de SSVEP voor relevante en irrelevante representaties voorspelden de mate waarin individuen in staat waren om afleiding te voorkomen. Daarentegen leverden de resultaten geen ondersteuning voor een selectieve rol van versterking van relevante, of verzwakking van irrelevante informatieverwerking, voor de mate waarin afleiding kon worden genegeerd. Om informatie goed te kunnen opslaan in de aanwezigheid van interferentie, lijkt het dus belangrijk om zowel de verwerking van relevante informatie te versterken, als ook de irrelevante informatie te onderdrukken.

Een tweede belangrijke bevinding in hoofdstuk 3 was dat aandacht mogelijk sequentieel focust op opgeslagen geheugenrepresentaties, potentieel als mechanisme om het geheugenspoor actief te houden (Awh et al., 1999; Postle, Awh, Jonides, Smith, & D'Esposito, 2004). De sequentiële of ritmische verdeling van aandacht over verschillende locaties is in voorgaand onderzoek alleen aangetoond tijdens perceptie (Dugué, Roberts, & Carrasco, 2016; Fiebelkorn, Saalmann, & Kastner, 2013), maar de mate waarin aandacht ook tijdens kortetermijngeheugen een vergelijkbare temporele dynamiek vertoont was tot nog toe onbekend.

Goede geheugenprestaties lijken op basis van de bevindingen uit zowel hoofdstuk 2, 3 als 4 dus af te hangen van het vermogen om sensorische activiteit geassocieerd met relevante en irrelevante representaties te kunnen aanpassen. Ten eerste lieten deze studies zien dat de modulatie van zowel regionale als representatie-specifieke sensorische activiteit een mechanisme is waarmee doelrelevante en irrelevante informatieverwerking kan worden gemoduleerd tijdens het inprenten en vasthouden van informatie in het kortetermijngeheugen. Dit mechanisme speelde zowel een rol in de af- als aanwezigheid van afleiding. Een tweede belangrijke bevinding in deze hoofdstukken is dat aandacht ook tijdens het vasthouden van informatie in het kortetermijngeheugen belangrijk is voor het goed kunnen vasthouden van geheugenrepresentaties. Dit werd gereflecteerd in de modulatie van sensorische activiteit die begon tijdens het opslaan van informatie in het kortetermijngeheugen, maar voortduurde tijdens het vasthouden van informatie, zelfs in de afwezigheid van expliciete instructies om aandacht te gebruiken.

In hoofdstuk 5, het laatste empirische hoofdstuk van dit proefschrift, werd onderzocht of en hoe verschillende vormen van irrelevante informatie uit de omgeving interfereren met de activatie en uitvoering van doelgerichte handelingen (Appelbaum, Smith, Boehler, Chen, & Woldorff, 2011; Nigbur et al., 2012). In deze studie werd een opzet gebruikt waarin proefpersonen gevraagd werd selectief te reageren op de kleur of bewegingsrichting van een bewegend, gekleurd stippenpatroon dat voor een korte tijd te zien was op het scherm. Terwijl proefpersonen dit deden werd hun hersenactiviteit geregistreerd met behulp van EEG. De essentiële manipulatie in deze opzet was dat de relevante en irrelevante stimulus dimensies (kleur; bewegingsrichting) op een deel van de trials 'incongruent' waren: de bewegingsrichting en kleur waren op deze trials geassocieerd met een verschillende respons. Tijdens het reageren op dit soort incongruente patronen is het nodig om de automatische activatie van de respons geassocieerd met de irrelevante dimensie te onderdrukken (van den Wildenberg et al., 2010). Dit gaat niet altijd goed: proefpersonen maken meer fouten en reageren trager op incongruente trials in vergelijking tot respons-congruente trials, ook wel het ‘conflict effect’ genoemd (Lu & Proctor, 1995; Simon & Rudell, 1967). Dit conflict effect vormt een maat van de interferentie tijdens de selectie van de doelrelevante respons.

De EEG-data in hoofdstuk 5 toonden aan dat het effect van respons conflict op gedrag, veroorzaakt door bewegingsrichting en kleur, geassocieerd was met een typische conflict-gerelateerde neurale respons die vooralsnog voornamelijk werd gevonden tijdens respons conflict veroorzaakt door stimulus locatie (Cohen & Donner, 2013). Deze respons betrof een snelle toename in de sterkte van theta activiteit (4-8 Hz) over midfrontale schedelgebieden. Om te toetsen of interferentie tijdens responsselectie specifiek afhankelijk is van de bron van interferentie (kleur of bewegingsrichting) werd onderzocht of de sterkte van het conflict effect veroorzaakt door bewegingsrichting en kleur vergelijkbaar was binnen proefpersonen. Dit was niet het geval: de mate van interferentie was specifiek voor de conflict-inducerende dimensie, en verschilde sterk tussen proefpersonen. Individuen die sterk werden afgeleid door de taak-irrelevante bewegingsrichting, werden in veel mindere mate afgeleid door de taak-irrelevante kleur van het patroon, en andersom. Deze individuele verschillen in het effect van respons conflict op gedrag waren bovendien gerelateerd aan de individuele conflict-gerelateerde theta respons per visuele dimensie. Deze resultaten vormden aanvullende ondersteuning voor het idee dat de mate van respons conflict in ieder geval deels afhankelijk is van de sensorische bron van interferentie, waarbij de mate van sensorische verwerking van taak-irrelevante informatie het succes voorspelt van de uitvoering van een doelgerichte handeling. De verwerking van dimensie-specifieke sensorische informatie is dus een bepalende factor in de mate waarin taak-irrelevante informatie interfereert met een voorgenomen doel.

Een meer algemene belangrijke bevinding in dit proefschrift was dat er systematische verschillen bestonden in de manier waarop individuele proefpersonen reageerden op de aanwezigheid van verschillende vormen van afleiding. Deze gedragsmatige verschillen werden gereflecteerd in individuele verschillen in selectieve aandacht tijdens kortetermijngeheugen, en in verschillen in de rekrutering van conflict-gerelateerde neurale mechanismen tijdens responsselectie. De neurale mechanismen betrokken bij het minimaliseren van afleiding werden soms pas duidelijk nadat individuele verschillen in de reactie op verschillende soorten afleiding in acht werden genomen (Vogel & Awh, 2008; Zilles & Amunts, 2013). Deze resultaten illustreren het belang van aandacht voor individuele verschillen in de cognitieve neurowetenschap.

Conclusies

Het onderzoek in dit proefschrift laat zien dat aandacht een belangrijke rol speelt in het kortetermijngeheugen en het voorkomen van responsconflict door het faciliteren van de selectieve verwerking van doelrelevante informatie in de aanwezigheid van interferentie. Aandacht faciliteert de inprenting en retentie van informatie in het kortetermijngeheugen in elk geval deels middels de continue aanpassing van sensorische informatieverwerking. Echter, de resultaten uit het onderzoek beschreven in dit proefschrift lieten ook zien dat de mate waarop verschillende soorten afleidende informatie interfereren met geheugenprestaties en responsselectie sterk varieert per individu. Een beter begrip van de verwerking en onderdrukking van afleidende informatie tijdens doelgericht gedrag levert op termijn hopelijk een bijdrage aan het verhelpen van verstoorde aandachtsprocessen bij mensen die hier problemen mee ervaren. Dit kan bijvoorbeeld door het aanpassen van de leefomgeving door afleiding die slecht kan worden uitgefilterd te minimaliseren, maar wellicht ook door de neurale verwerking van irrelevante informatie van buitenaf te beïnvloeden, met bijvoorbeeld hersenstimulatie.

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