Flexible updating of visual working memory

– The joint roles of attention and action

Dissertation
zur Erlangung des Doktorgrades der Naturwissenschaften
(Dr. rer. nat.)

dem Fachbereich Psychologie der Philipps-Universität Marburg
vorgelegt von

Anna Heuer
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Marburg an der Lahn, Juli 2016

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CONTENTS

SUMMARY

Visual working memory allows us to retain information over short periods of time, thereby enabling the comparison of objects separated in time or space. This ability is critical for various tasks, but it is highly limited in capacity (e.g., Luck & Vogel, 2013). As visual information constantly gains or loses relevance as we interact with our environment, there is a need to update the contents of visual working memory in a flexible manner to ensure that its limited capacity is used efficiently. In five studies, this dissertation examined how this updating is accomplished.

The first part of this dissertation (Studies I-III) investigated updating following cues presented during visual working memory maintenance. These so-called retrocues indicate some memorized items as more task-relevant than others, inducing a strategic internal orienting of attention and thereby improving memory (e.g., Griffin & Nobre, 2003). Study I examined whether this internal deployment of attention can be used to update the contents of visual working memory to reflect graded differences in relevance. It was found that memory for the most task-relevant and thus continuously attended representations was improved, and that this benefit was related to the individual efficiency of attentional control. Performance for less task-relevant and intermittently unattended information was worse, but still well above chance level. These findings show that the contents of visual working memory can be flexibly weighted according to their relevance: While particularly important information is robustly maintained inside the focus of attention, less important information can be kept available in a more fragile, unattended state.

Studies II and III investigated whether visual working memory updating is also flexible with respect to the visual characteristics that can be used to guide attentional selection. Retrocues relying on different stimulus characteristics (directly or symbolically indicated location, colour and shape) were found to be effective, revealing that the attentional selection of representations can operate on whichever visual property carries information about task-relevance. Drawing on what is known about attention to perceptual events (Carrasco, 2011), Studies II and III further established that a basic distinction can be drawn between mechanisms of spatial and feature-based selection. Study II dissociated these two mechanisms behaviourally: While feature-based retrocues yielded benefits for items presented at both contiguous and non-contiguous locations, spatial retrocues only improved performance for items at contiguous locations. This suggests that feature-based attention operates in a global fashion, enhancing representations throughout the spatial layout of visual working memory, whereas spatial attention cannot as easily access non-contiguous representations. Study III further corroborated the notion of distinct mechanisms for spatial and feature-based selection by

dissociating these at the cortical level using transcranial magnetic stimulation. Whereas stimulation of the supramarginal gyrus selectively facilitated spatial selection, stimulation of the lateral occipital cortex selectively facilitated feature-based selection. Seeing as the same brain areas have been implicated in spatial and feature-based attention to perceptual events (e.g., Murray & Wojciulik, 2004; Schenkluhn et al., 2008), this also indicates that these two mechanisms of selective attention recruit overlapping neural networks when operating over perceptual input and mnemonic representations.

The second part of the dissertation looked at the effects of more natural indicators of the relevance of specific aspects of our visual surroundings: actions and action-intentions. Instead of presenting retrocues during visual working memory maintenance, Studies IV and V used dual-task paradigms, in which an action was to be executed or prepared. This action rendered some items in a concurrently performed memory task more potentially relevant than others. Action and attention are tightly linked (e.g., Baldauf & Deubel, 2010), and preparing a particular action was expected to induce an attentional updating of visual working memory to weight its contents according to their action-relevance. The investigation of such an action-induced updating of visual working memory built on two mechanisms of selective action-related processing that have been shown to modulate visual perception: the deployment of spatial attention to action goals (e.g., Baldauf, Wolf, & Deubel, 2006; Study IV), and the weighting of action-relevant feature dimensions (e.g., Memelink & Hommel, 2013; Study V).

Study IV revealed that representations corresponding to an action goal are preferentially maintained: Performance for items that had been presented at the location of an action goal in an otherwise unrelated movement task performed during the maintenance interval was better than for items presented at action-irrelevant locations. This effect was observed when memory load was at the average capacity limit, suggesting that information holding potential relevance for an action is prioritized when demand on the system is high. The effect of the allocation of attention to an action goal was spatially not specific to that location. Instead, there was an attentional gradient spreading out from the action goal location, as indicated by decreasing performance with increasing distance.

Study V drew on the finding that preparing an action primes feature dimensions that are relevant for that particular action, increasing the impact of these dimensions on perceptual processing (e.g., Wykowska, Schubö & Hommel, 2009), and showed that this effect of action intentions continues beyond the perceptual stage: Memory for items coded on action-relevant feature-dimensions was better than for items coded on action-irrelevant feature dimensions. Specifically, memory for size was found to be better during the preparation of a grasping movement, whereas memory for colour tended to be better during the preparation of a pointing movement. This weighting reflects the action-relevance of these feature dimensions. Whereas size is relevant for preparing a grasp, colour can be used to localize a goal object and guide a pointing movement.

In sum, the present dissertation demonstrates that updating of visual working memory is remarkably flexible. Maintained information can be weighted to reflect graded differences in relevance (Studies I-V), irrespective of whether this relevance is explicitly indicated by external cues (Studies I-III) or more implicitly indicated by action intentions (Studies IV and V). Different representational characteristics can guide the selection of relevant memory contents: Updating is induced when some representations are more important than others because they correspond to relevant locations (Studies I-IV) or because they contain a feature, which is more relevant than other features of the same dimension (Studies II and III) or coded on a feature dimension that is more relevant than other dimensions (Study V). This flexibility highlights the versatile nature of visual working memory, which allows for an efficient use of its highly limited capacity in any given situation.

1

INTRODUCTION

The sensory experiences guiding our behaviour are dominated by vision, and it is not just what is right in front of our eyes that matters, but also what is left of it in our inner worlds in the form of representations in memory. Vision scientists habitually point out that the visual system is confronted with an overwhelming amount of information at any given moment, but in fact, there are moments when visual input is interrupted. This is for instance the case when we move our eyes, which happens about three times per second. In these moments, we rely on internal representations of our visual surroundings. Visual working memory is the part of the visual system that allows us to retain and manipulate information over short periods of time, thereby enabling comparison operations of objects separated in time or space. Such operations are involved in simple everyday tasks, for example in establishing correspondence across eye movements, but they are also important for other cognitive functions such as object recognition or the learning of object categories, and individual measures of working memory are associated with intelligence and performance on numerous cognitive tasks (Conway, Kane, & Engle, 2003; Fukuda, Vogel, & Mayr, 2010; Johnson et al., 2013).

Even though maintaining visual information underpins a range of cognitive processes and behaviours, this ability is highly limited. The capacity of visual working memory is currently conceptualized as being limited either by a resource that can be flexibly distributed among a theoretically infinite number of items (Bays, Catalao, & Husain, 2009; Bays & Husain, 2008; Ma, Husain, & Bays, 2014) or by a number of discrete slots that only allows for the maintenance of three to four items on average (Cowan, 2001; Luck & Vogel, 1997, 2013; Zhang & Luck, 2008). While the exact nature of visual working memory capacity remains an active area of debate, this limitation necessitates selective processing to ensure that only relevant information is maintained.

Attention is the mechanism that allows for such selective processing by enhancing the relevant and suppressing irrelevant information. While traditionally, the influence of selective attention on visual working memory was thought to end after encoding, more recent research has shown that attentional modulation continues throughout all processing stages up to retrieval (Gazzaley & Nobre, 2012). The importance of a continuous modulation becomes evident when we think of the way visual working memory operates in everyday life. In the laboratory, a certain set of stimuli is typically relevant for the duration of a trial, and is then followed by a new set of stimuli to be memorized. Outside the laboratory, however, there are no such discrete intervals. Rather, information already maintained in visual working memory gains or loses relevance depending on our behavioural goals that are constantly changing as we interact with our visual environment. An efficient use of the limited capacity of visual working memory therefore requires flexible updating in accordance with changes in the relevance of maintained information. The present dissertation aimed at understanding how this updating is accomplished.

1.1 Attentional modulation of maintenance in visual working memory

The notion of a flexible updating of visual working memory by selective attentional modulation implies that not all maintained information is necessarily also attended, but that attention can instead be devoted to or withdrawn from specific memory contents. From a historical perspective, this is by no means a trivial insight, given that working memory has traditionally mostly been conceived of as the set of elements from long-term memory that are currently activated or in one's focus of attention and awareness (e.g., James 1890; for an overview see Cowan, 1995). More recent models conceptualize working memory as a store in which information can be maintained in various states of activation, positing that there is an internal focus of attention within working memory (Cowan, 1993; LaRocque, Lewis-Peacock, & Postle, 2014; McElree, 1998; Oberauer, 2002; Olivers, Peters, Houtkamp, & Roelfsema, 2011). These state-based models make competing claims with respect to how many different states there are and how many items can be in the focus of attention, but the basic idea that information can be maintained in different representational states and that these states are established by attention has by now received substantial empirical support (LaRocque, Lewis-Peacock, Drysdale, Oberauer, & Postle, 2013; LaRocque et al., 2014; Lewis-Peacock, Drysdale, Oberauer, & Postle, 2012; Nee & Jonides, 2008, 2011, 2013; Zokaei, Manohar, Husain, & Feredoes, 2014).

For the visual modality, the deployment of attention towards maintained information can be selectively manipulated using so-called retrocues (for an overview see Souza & Oberauer, 2016), which were first introduced by Griffin and Nobre (2003). They had participants perform a typical visual working memory task, for which they had to memorize a number of items (memory items) to compare against a test stimulus presented after a retention interval. During the retention interval, a cue spatially indicated a location at which previously a memory item had been presented, thereby retroactively orienting attention to that item. Importantly, retrocues are presented well after the decay of the iconic trace, ensuring that they operate on representations in visual working memory and not in iconic memory (Irwin & Thomas, 2008). Griffin and Nobre (2003) found that valid retrocues yielded a benefit in terms of both accuracy and reaction time, whereas invalid retrocues were associated with costs in performance as compared to a neutral condition, in which the retrocue provided no information about the relevance of specific items. A large number of studies have since replicated these behavioural effects (e.g., Astle, Summerfield, Griffin, & Nobre, 2012; Lepsien, Griffin, Devlin, & Nobre, 2005; Lepsien, Thornton, & Nobre, 2011; Lepsien & Nobre, 2007), and established that it is indeed possible to orient attention to representations in visual working memory, affecting the availability of representations within and outside the focus of attention.

It has proven particularly fruitful to study the deployment of attention to internal representations in relation to the already much better understood deployment of attention to external events. Experimentally, comparability between these two domains of attentional orienting (memory and perception) can be established in a straightforward fashion, namely by presenting cues either after the appearance of items to be memorized (retrocues) or before (precues), as in a classical spatial cueing paradigm (Posner, 1980). Mnemonic (internal) attention has been shown to be remarkably similar to perceptual (external) attention in terms of behavioural benefits and costs associated with valid and invalid cueing, and also with respect to the neural network of frontal, parietal and occipital areas that is involved (e.g., Dell'Acqua, Sessa, Toffanin, Luria, & Jolicoeur, 2010; Griffin & Nobre, 2003; Lepsien et al., 2005; Lepsien & Nobre, 2007; Nee & Jonides, 2009; Nobre et al., 2004; Poch, Campo, & Barnes, 2014). In spite of these commonalities, there are also notable differences, indicating that internal attention exhibits its own distinct characteristics. For instance, unlike external attention, shifts of internal attention appear not to be induced by peripheral cues (Berryhill, Richmond, Shay, & Olson, 2012) or to be influenced by the physical distance between objects at encoding (Tanoue & Berryhill, 2012). At the neural level, brain imaging and stimulation studies have revealed stronger activations in parietal regions and the selective engagement of certain frontal regions when attention is oriented within visual working memory (Nobre et al., 2004; Tanoue, Jones, Peterson, & Berryhill, 2013). It is thus unlikely that there is a single attentional mechanism underlying selection in perception and in working memory (see also Chun, Golomb, & Turk-Browne, 2011).

1.1.1 Focused and defocused representations

The exact mechanisms by which attending to internal representations improves performance are still poorly understood. In analogy to what is known about external attention (Carrasco, 2011), one could assume that the relevant representations that are attentionally selected are enhanced, whereas irrelevant representations are inhibited. Indeed, for the selected (focused) representations, the deployment of attention within visual working memory is highly advantageous: representations in the focus of attention have been shown to be in a privileged and particularly robust state. More specifically, they are protected from degradation over time (Matsukura, Luck, & Vecera, 2007) and resistant to interference from novel incoming stimuli (Landman, Spekreijse, & Lamme, 2003; Makovski & Jiang, 2007; Makovski, Sussman, & Jiang, 2008; Pertzov, Bays, Joseph, & Husain, 2013; Sligte, Scholte, & Lamme, 2008; Sligte, Vandenbroucke, Scholte, & Lamme, 2010). The representational quality itself appears not to be improved, but the likelihood of recall is increased to the extent that information which would otherwise be irretrievable can be restored (Murray, Nobre, Clark, Cravo, & Stokes, 2013).

While it is well-established that attention benefits the focused representations, the fate of the nonselected (defocused) representations is less clear. Some evidence favours the idea that defocused representations remain available, but that maintenance outside the focus of attention leaves them subject to faster decay (Janczyk, Wienrich, & Kunde, 2008; LaRocque et al., 2013; Lewis-Peacock et al., 2012; Rerko & Oberauer, 2013). Impaired memory for defocused as compared to focused items has been taken to reflect passive forgetting over time (Janczyk et al., 2008; Rerko & Oberauer, 2013) or enhanced forgetting (Pertzov et al., 2013) consistent with inhibition.

Other authors have gone one step further and suggested that defocused representations are actively removed from memory, thereby reducing memory load and the inter-item competition for resources (Astle et al., 2012; Kuo, Stokes, & Nobre, 2012). Kuo, Stokes, and Nobre (2012) found that a lateralized event-related potential (ERP) of the EEG associated with the number of items maintained in visual working memory, the Contralateral Delay Activity (CDA, also called Sustained Posterior Contralateral Negativity (SPCN), see Jolicoeur, Sessa, Dell'Acqua, & Robitaille, 2006, or Contralateral Negative Slow Wave (CNSW), see Klaver, Talsma, & Wijers, 1999; in the following referred to as CDA/SPCN), was reduced after a valid retrocue, from which the authors concluded that the noncued items were discarded. Importantly, however, these items were never actually tested in their experiments, so that no definite conclusions can be drawn with respect to whether or not these items were still available. A disappearance of neural markers associated with noncued items was also observed by two studies using multivariate pattern analysis of delay activity recorded by functional magnetic resonance imaging (fMRI; Lewis-Peacock et al., 2012) and EEG (LaRocque et al., 2013), but the behavioural results revealed that these items were nevertheless remembered. Their neural signatures were even reactivated when a second retrocue required their refocusing, suggesting that persistent delay activity might reflect the maintenance of items within the focus of attention, but that it is not needed for maintenance per se. Accordingly, on the one hand, the findings of Kuo et al. (2012) are not necessarily inconsistent with the notion that defocused representations remain in visual working memory and are maintained outside the focus of attention. On the other hand, the very fact that uncued items were never tested by Kuo et al. (2012) might indeed have led to their removal. In a similar paradigm, Williams, Hong, Kang, Carlisle, and Woodman (2013) tested uncued items on a small number of trials and unbeknownst to participants. Performance for these items was at chance level, indicating that they had been discarded from memory following the allegedly always valid retrocues.

Taken together, these findings point to a factor that might be crucial in determining the fate of defocused representations: the validity of the retrocues, or rather the likelihood of uncued items to become task-relevant again. Consistently valid retrocues create a situation in which information is either relevant or absolutely irrelevant. Removing any uncued information is therefore highly beneficial for an efficient use of visual working memory, because it frees capacity for the maintenance of more important information. But given that a selection of relevant information already occurs for encoding (Gazzaley & Nobre, 2012), the situation in which some of the information that was important at encoding is rendered entirely irrelevant shortly thereafter during maintenance is rather unlikely to be frequently encountered outside the laboratory. What might better reflect the demands on visual working memory in natural environments is that some information is more relevant for current purposes, warranting attentional protection, while other information might still be important in the future and thus worth holding on to. Study I examined the fate of defocused representations in such a scenario, in which the respective items may become task-relevant again, but only in addition to other, more relevant and thus continuously focused items.

1.1.2 Spatial and feature-based attentional selection

For an optimal use of the visual system, it is important that selective processing can flexibly rely on different types of information, because different visual properties can carry information about the relevance of certain objects in our environment. Imagine, for instance, that you are picking up a friend at the station. She said she would wait by the main entrance, so you will focus your search on that area – *location* renders the visual information in that part of your surroundings relevant for your current purpose. You also expect her to wear her green jacket, so you will scan that area for green objects – here, your search is guided by *colour*.

For external attention, it has been established that essentially all sorts of stimulus characteristics can be used to guide the deployment of attention. This can for example be features such as colour, orientation or movement direction (e.g., Bichot, Rossi, & Desimone, 2005; Martinez-Trujillo & Treue, 2004; Maunsell & Treue, 2006; Saenz, Buracas, & Boynton, 2002), conjunctions of features (e.g., Buracas & Albright, 2009; Nordfang & Wolfe, 2014; Weidner & Müller, 2013), spatial locations (Carrasco, 2011; Posner, 1980) or categories of more complex objects such as faces or houses (e.g., Serences, Schwarzbach, Courtney, Golay, & Yantis, 2004; Theeuwes & Van der

Stigchel, 2006). A distinction is typically drawn between spatial and feature-based attention. These have been shown to differ with respect to behavioural consequences and neural mechanisms and can accordingly, at least to some extent, be regarded as distinct attentional mechanisms (Carrasco, 2011).

The investigation of internal attention has so far largely neglected whether it can operate on different stimulus characteristics. Most studies used either spatial retrocues, that is, retrocues that spatially indicated specific locations at which memory items had previously been presented (e.g., Astle, Nobre, & Scerif, 2012; Astle et al., 2012; Poch et al., 2014), or retrocues that indicated entire object categories such as faces and scenes (Lepsien & Nobre, 2007; Lepsien et al., 2011). Flexibility with respect to the type of stimulus characteristic that can be used for attentional guidance would be no less important for internal attention than for external attention. But the few studies that did test the efficacy of retrocues relying on different kinds of information have led to mixed results. Berryhill, Richmond, Shay, and Olson (2012) were the first to compare different types of retrocues. While a typical spatial arrow retrocue yielded a behavioural benefit, no benefits were observed for either a peripheral retrocue presented at the location of an item, or for a more symbolic spatial retrocue that consisted of a number mapping onto a location. It should be noted, however, that some experimental details might have precluded the successful use of especially a more symbolic retrocue, which presumably required more time or additional effort to be processed. First evidence that retrocues based on stimulus characteristics other than spatial location can indeed be used to guide internal attention was provided by Pertzov, Bays, Joseph, and Husain (2013) and Li and Saiki (2014), who found that retrocueing an object's colour was just as advantageous as retrocueing it's spatial location. Studies II and III built on these findings and systematically tested different types of spatial and feature-based retrocues to establish whether the internal selection of visual working memory representations can flexibly rely on different stimulus characteristics.

One concern with feature-based retrocues is that they might only be used to retrieve information about the object's location, recoding featural into spatial information (Pertzov et al., 2013). In effect, these different types of retrocues would then rely on the same mechanism: spatial attention. To examine whether this is indeed the case, or whether, instead, different attentional mechanisms are involved, one can draw on differences between spatial and feature-based attention that have been established for external attention. For one, external spatial and feature-based attention have been shown to differ with respect to access to non-contiguous locations in the visual field. Feature-based attention operates in a spatially global fashion, modulating feature-specific neural activity throughout visual cortex and thereby enhancing performance for stimuli with a shared relevant feature across the visual field, independent of the spatial locus of attention (Maunsell & Treue, 2006; Saenz et al., 2002; Sàenz, Buraĉas, & Boynton, 2003; Treue, 2003). It is still being debated whether spatial attention can be split and allocated to multiple separate locations as well, but a large body of evidence indicates that this is, at the very least, not as easily achieved as with feature-based attention (Cave, Bush, & Taylor, 2010a, 2010b; Eimer & Grubert, 2014; Jans, Peters, & De Weerd, 2010a, 2010b). Building upon this difference between spatial and feature-based attention when it comes to enhancing processing at separate locations, Study II tested whether spatial and feature-based retrocues differed with respect to parallel access to representations of items presented at contiguous and separate, non-contiguous locations.

External spatial and feature-based attention further differ with respect to the underlying neural networks. While the involved networks are largely overlapping, spanning areas in frontal, parietal and occipital cortex, subregions or populations of neurons within these networks have been identified as preferential or specific for either type of selective attention (Giesbrecht, Woldorff, Song, & Mangun, 2003; Greenberg, Esterman, Wilson, Serences, & Yantis, 2010; Schenkluhn, Ruff, Heinen, & Chambers, 2008; Slagter et al., 2007; Vandenberghe, Gitelman, Parrish, & Mesulam, 2001). Study III sought to corroborate the notion of analogous distinct mechanisms for internal spatial and feature-based attention by dissociating these mechanisms at the cortical level.

1.2 Action-induced effects on visual working memory

As outlined above, the weighting and updating of visual working memory contents has typically been studied by presenting cues to indicate which maintained information is important and which is not. While this experimental procedure may have its counterparts in everyday life, for instance when we think of road signs instructing us to pay attention to certain parts of the environment, its ecological validity is limited. We are almost continuously engaged in some sort of action, and which aspects of our visual environment are most relevant to us is mainly determined by what we are currently intending to do. Even in the experimental situation, a cue loses its significance as soon as one does not intend to perform the action as instructed, namely to press the correct button in the visual working memory task.

The role of actions and action intentions for the selective processing of visual information has been acknowledged for a while now, and the visual system has been postulated to be a system specifically optimized for gathering the information that is required for movement planning and parameter specification (Allport, 1987; Neumann, 1987). The influence of actions on selective visual processing has been established for perception, but the filtering of relevant from irrelevant information clearly continues to be important beyond the perceptual stage. The role of actions and action planning for the selective maintenance of information over short periods of time was examined in the second part of this dissertation project. Because the influence of actions on visual working memory maintenance has never been systematically studied before, this investigation largely drew on what is known about action-induced effects on perception. More specifically, it built on two mechanisms of selective action-related processing that have been shown to influence perception: the deployment of spatial attention to action goals, and the selective weighting of action-related feature dimensions.

1.2.1 Deployment of spatial attention to action goals

Goal-directed actions require that all the relevant visuo-spatial information about the goal object (e.g., its location, size, surface texture or orientation) is extracted and preferentially processed. The deployment of spatial attention to action goal locations is one mechanism whereby this enhanced processing of action-relevant information is accomplished.

The allocation of attention to an action goal has mostly been studied with dual-task paradigms, in which participants were to perform a particular movement in combination with a visual task that required the detection, discrimination or identification of a target stimulus presented briefly before the movement was initiated. Early research focused on saccadic eye movements, and showed that performance for visual targets presented at the saccade goal was better than for targets presented at action-irrelevant locations (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995). Notably, this pattern was even observed when participants knew in advance where the visual target would be presented, indicating that they were unable to attend to a location other than the saccade goal (Deubel & Schneider, 1996).

Given that the link between the oculomotor system and attention is particularly strong (Awh, Armstrong, & Moore, 2006; Maurizio Corbetta et al., 1998; Rizzolatti, Riggio, Dascola, & Umiltà, 1987), it is not self-evident that a similar relation would also exist for the skeletomotor system, but remarkably similar findings have been obtained for hand movements (for a review, see Baldauf & Deubel, 2010). During the preparation of pointing movements, perceptual performance is best when the location of the visual target corresponds to the action goal location (Baldauf & Deubel, 2008b, 2009; Baldauf, Wolf, & Deubel, 2006; Deubel, Schneider, & Paprotta, 1998). Enhanced processing of visual information at the action goal location occurs irrespective of participants' knowledge of the location of the visual target (Deubel et al., 1998). Thus, the coupling of spatial attention to an action goal appears to be obligatory in that it is not possible to attend away from the goal location during the preparation of an action, even when there is an incentive (e.g., the presentation of a perceptual target at another location) to do so.

In order to gather the potentially relevant information at the action goal location, the deployment of attention should ideally be spatially very specific to that location. This would reduce interference from surrounding action-irrelevant objects, and it would ensure that attention is not distributed over an unnecessarily large region of the visual field, thereby decreasing processing efficiency (Castiello & Umiltà, 1990; Müller, Bartelt, Donner, Villringer, & Brandt, 2003). Indeed, a high spatial specificity has been demonstrated for manual pointing movements (Baldauf et al., 2006; Deubel et al., 1998). When an action involves multiple movement goals, attention is not uniformly distributed over a larger region of the visual field comprising all goal locations. Instead, goal locations are selected by spatially distinct foci of attention in a parallel fashion, leaving intermediate locations unattended. This has been shown for bimanual pointing movements (Baldauf & Deubel, 2008b), sequences of pointing movements (Baldauf & Deubel, 2009; Baldauf et al., 2006), and for grasping movements (Baldauf & Deubel, 2010; Schiegg, Deubel, & Schneider, 2003; here, the movement goals are the different target positions of the fingers involved in a grasp, see Smeets & Brenner, 1999).

An equivalent enhancement as observed for perceptual representations of visual stimuli at action goal locations might be expected for visual working memory representations corresponding to goal locations. Similar to retrocues spatially indicating specific items as more important than others, performing an action during the retention interval should spatially highlight an item previously presented at the action goal location as potentially (action-)relevant. Study IV investigated whether representations in visual working memory are weighted according to differences in their potential action relevance as indicated by a spatial correspondence with an action goal.

1.2.2 Selective weighting of action-related feature dimensions

Allocating spatial attention to the goal object ensures that visual information relating to that object is preferentially processed over other objects in the visual environment. But depending on what exactly it is that we want to do with that object, different features matter. Imagine a banana in a fruit bowl that is on a table in front of you. If you want to grab and eat that banana, you need to consider its size and its orientation, because these features affect the posture of your hand (i.e., grip aperture and orientation) that is optimal for grasping it. By contrast, if you want to point out to your friend that there is a banana left in the bowl, size and orientation are irrelevant. But you need to localize it so your finger is pointing in the right direction, and the banana's yellow colour and greater luminance compared to some surrounding apples and dark grapes might be useful for doing so. In these two scenarios, the visual information and the goal object are the same, but our action intentions render different features more relevant than others. These differences in action-relevance have been shown to affect perception: Setting up a particular action plan primes action-related feature dimensions by increasing their weight and thus their impact on perceptual processing. This mechanism of selective action-related processing is referred to as *intentional weighting* (Hommel, Musseler, Aschersleben, & Prinz, 2001; Hommel, 2009; Memelink & Hommel, 2013).

For one, action planning enhances the processing of action-relevant features of the goal object itself. For instance, Bekkering and Neggers (2002) asked participants first to look for and saccade to a target object, and then to perform a predefined action: to either grasp or point to the very same object. This target was defined by a conjunction of orientation and colour, and presented among distractors. Participants made fewer orientation errors, which were defined as the percentage of trials in which the first saccade was made to a distractor with the wrong orientation, when they were planning a grasping movement than when they were planning a pointing movement. The authors propose that orientation selection was improved in these trials because this feature of the target object was relevant for the intended grasping action. Hannus, Cornelissen, Lindemann, and Bekkering (2005) used the same design, but two-dimensional stimuli presented on a screen instead of three-dimensional objects as targets. A selective enhancement of orientation processing was observed even under these quite unnatural conditions, when the goal objects were to be ‘grasped’ on a screen.

Action planning involves not only the enhanced processing of action-relevant features of the goal object, but the priming of entire feature dimensions that provide action-relevant information. The stronger weighting then increases the impact of all features coded on these dimensions on perceptual processing. This more general effect of intentional weighting has been demonstrated by studies combining a movement task with an unrelated visual task. In a study by Fagioli, Hommel, and Schubotz (2007), participants were presented with a sequence of stimuli while they were preparing either a grasping or a pointing movement to an object placed in front of them. The sequentially presented stimuli predictably varied in location or size, and the task was to detect the target stimulus that deviated from the pattern. Even though the two tasks were entirely unrelated, preparing a pointing movement facilitated the detection of targets that deviated in location, and preparing a grasping movement facilitated the detection of targets defined by size. Using a similar design, but a visual search task that required the selection of targets in space (and not in time, as in the study by Fagioli et al., 2007), Wykowska, Schubö, and Hommel (2009) found that the detection of luminance targets was facilitated when participants were planning a pointing movement, whereas the detection of size targets was facilitated when they were planning a grasping movement. Thus, intentional weighting of feature dimensions does not only affect selection processes relating to the action goal object, but even early stages of perceptual and attentional processing during action planning (see also Wykowska & Schubö, 2012). Such a weighting can even be induced exogenously and without active action planning, for instance by having participants watch videos of particular actions being performed (Fagioli, Ferlazzo, & Hommel, 2007).

So what if you are busy pouring tea when your friend asks you if there is a banana left in the bowl, and you want to point it out to him without looking up? Experience tells us that this task is not too difficult, and Study V investigated whether this ease with which you will most likely point to the banana can at least partially be attributed to a selective weighting of representations in visual working memory according to specific action intentions.

1.3 Aims and experimental approaches

The aim of this dissertation was to understand how the contents of visual working memory can be flexibly updated and weighted to reflect differences in their relevance to current behavioural goals. The first part of the dissertation (Studies I – III) examined how this can be achieved by explicitly orienting attention to certain representations following cues that provide information about their task-relevance. The second part (Studies IV and V) investigated whether a more natural indicator of task-relevance, namely actions and action intentions, also induces a weighting of maintained information.

Study I

Study I examined whether representations in visual working memory can be weighted according to differences in their task-relevance. More specifically, we were interested in the fate of defocused items, that is, items that are intermittently marked as less task-relevant than other items and presumably removed from the internal focus of attention. Previous studies have shown that performance for these items is impaired (e.g., Janczyk et al., 2008; Rerko & Oberauer, 2013), and it has even been suggested that they are removed from memory (Astle et al., 2012; Kuo et al., 2012). As outlined above, Study I was motivated by the idea that task context might be a crucial factor in determining the fate of defocused items. Valid retrocues render the items not indicated by the cue absolutely irrelevant. This means that the removal of these consequently defocused items would indeed be the most efficient strategy. However, this situation is quite artificial: there are control processes that regulate access to visual working memory, ensuring that only relevant information gets in (e.g., Gazzaley & Nobre, 2012; Vogel, McCollough, & Machizawa, 2005), and it is rather unlikely that information that was important at encoding loses all relevance shortly thereafter. A situation that is probably more frequently encountered in natural environments is that some information is currently more relevant, justifying attentional protection, while other information potentially still holds some relevance and is thus worth holding on to. To reflect this situation, Study I used a double-retrocue paradigm. The first retrocue always indicated two of four previously presented memory items as task-relevant. The second retrocue presented during the retention interval either marked the same two items (Hold condition), or it additionally marked one (Add1 condition) or two adjacent items (Add2 condition). Thus, the two items indicated by the first retrocue were always task-relevant (continuously focused), but there was still some likelihood that the initially uncued (intermittently defocused) items would become relevant again upon presentation of the second retrocue. A neutral retrocue condition served as a baseline for performance when no subset of information was focused. For one, we were interested in whether defocused items would remain available in this scenario, and if so, if a cost would be associated with defocusing. Moreover, building on research highlighting a relationship beween individual attentional control and visual working memory functions (e.g., Fukuda & Vogel, 2009, 2011; Vogel et al., 2005), we examined whether the magnitude of the retrocueing benefit is related to the individual efficiency of attentional selection.

To answer these questions, behavioural performance and two ERP components associated with maintenance in visual working memory (CDA/SPCN) and the efficiency of attentional selection (N2pc) were analysed. The CDA/SPCN and the N2pc are lateralized components that appear as enhanced negativities at posterior electrode sites contralateral to the respective visual hemifield. The N2pc can be observed approximately 200 – 300 ms after stimulus onset (Eimer, 1996; Luck & Hillyard, 1994). It is sensitive to the number of selected items, increasing in amplitude with an increasing number, and to individual behavioural efficiency (Drew & Vogel, 2008; Mazza & Caramazza, 2011; Mazza, Pagano, & Caramazza, 2013; Pagano, Lombardi, & Mazza, 2014; Pagano & Mazza, 2012). The CDA/SPCN appears about 300 ms after stimulus onset and usually persists throughout the maintenance period (e.g., McCollough, Machizawa, & Vogel, 2007). Its amplitude has been shown to reflect the number of items maintained in visual working memory, reaching an asymptote at around mean capacity limit (Luria, Balaban, Awh, & Vogel, 2016; Vogel & Machizawa, 2004).

If defocused items were excluded to reduce memory load, then performance for these items should be close to chance level, and CDA/SPCN amplitude in the cued conditions should be attenuated following the first retrocue as compared to the neutral condition. If, in contrast, defocused items remained available, performance for these items should be well above chance level, and they could be refocused upon presentation of the second retrocue. Differential focusing and weighting of items was expected to reflect in diverging CDA/SPCN amplitude after the second compared to after the first retrocue. If a cost was associated with defocusing items, then performance for the intermittently defocused items should be worse than for the continuously focused items. Alternatively, refocusing could 'boost" these items up the level of continuously focused items, and accordingly performance for these two item types should be equivalent. Moreover, the comparison of performance for the continuously focused items in the Hold condition with performance for the continuously focused items in the Add conditions will clarify whether the inclusion of additional items in the internal focus of attention (i.e., the inclusion of the intermittently defocused items in the Add conditions) affects maintenance of items already in the focus of attention (i.e., maintenance of the continuously focused items in the Add conditions as compared to in the Hold condition).

To establish whether the magnitude of the retrocueing benefit is related to individual attentional efficiency, correlations between the N2pc modulations following each retrocue and the behavioural retrocueing benefits were computed. We expected that stronger N2pc modulations, indicating higher attentional efficiency, would be associated with larger retrocueing benefits.

Study II

Study II investigated whether attention can update and modulate the contents of visual working memory operating on features just as well as on locations. Whereas it has long been established that different stimulus characteristics can be used to guide attention in the external world (Carrasco, 2011), the investigation of attention to representations in memory has almost exclusively relied on spatial cues to locations at which maintained items had previously been presented (e.g., Astle et al., 2012; Griffin & Nobre, 2003). But especially for the capacity-limited visual working memory system (Luck & Vogel, 2013), it would be highly advantageous if attentional modulation could flexibly rely on whatever type of information is available about the relevance of certain aspects of our visual environment. To examine whether this is possible, different types of retrocues were presented during the retention interval of a visual working memory task, for which participants had to memorize orientations (Experiment 1) or colours (Experiment 2): a spatial retrocue (an octagram with blackened corners pointing towards locations), a symbolically spatial retrocue (numbers mapping onto locations) and feature-based retrocues (a blob of the colour of maintained items in Experiment 1, and an outline of the shape of maintained items in Experiment 2). Based on two studies reporting benefits for nonspatial retrocues (Li & Saiki, 2014; Pertzov et al., 2013) and on the high degree of similarity between external and internal attention outlined above, we expected improved performance for all retrocue types relative to a neutral condition, in which the retrocue provided no information as to the relevance of specific items.

To test whether the different retrocue types relied on different attentional mechanisms (spatial and feature-based attention, that is), we examined differences with respect to access to representations of items presented at contiguous and non-contiguous locations. For the perceptual domain, it has been shown that feature-based attention can be allocated to multiple separate locations, enhancing the processing of relevant stimuli across the entire visual field (e.g., Maunsell & Treue, 2006; Saenz et al., 2002; Sàenz et al., 2003; Treue, 2003). Spatial attention, in contrast, cannot be as easily split and allocated to non-contiguous locations (e.g., Jans et al., 2010b). In both experiments of Study II, the retrocues always indicated two items that had been presented at either neighbouring (contiguous) or non-neighbouring (non-contiguous) locations. Whereas for feature-based retrocues, we predicted retrocueing benefits irrespective of the spatial configuration of the cued items, we expected benefits for neighbouring cued items, but attenuated or no benefits for non-neighbouring cued items with spatial retrocues. This pattern of results would indicate that internal feature-based and spatial attention rely on different mechanisms, similar to what is known about external attention (Carrasco, 2011).

Study III

Study III built on Study II and sought to further corroborate the notion of distinct mechanisms for spatial and feature-based attentional selection in visual working memory. Whereas Study II drew on established differences in the behavioural signatures of external spatial and feature-based attention, Study III aimed at dissociating these mechanisms at the cortical level. For external attention, feature-based and spatial attention have been shown to recruit largely overlapping neural networks involving frontal, parietal and occipital cortex, but subregions or populations of neurons within these networks are preferential or specific for either type of selective attention (Giesbrecht et al., 2003; Greenberg et al., 2010; Schenkluhn et al., 2008; Slagter et al., 2007; Vandenberghe et al., 2001). In Study III, we used transcranial magnetic stimulation (TMS) to identify areas in parietal and occipital cortex that are specifically involved in spatial and feature-based attention to visual working memory representations.

During the retention interval of a task requiring the memorizing of the colours of three items, a retrocue was presented that indicated one of the maintained items as relevant either by its location (spatial attention) or by its shape (feature-based attention). Based on previous studies (Li & Saiki, 2014; Pertzov et al., 2013; Study II) we expected retrocueing benefits as compared to a neutral retrocue condition. During cue presentation, TMS was applied to the supramarginal gyrus (SMG) and the lateral occipital cortex (LO). Whereas SMG has been implicated in the control of external spatial attention (Chambers, Stokes, & Mattingley, 2004; Schenkluhn et al., 2008), extrastriate visual cortex has been shown to be involved in external feature-based attention (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991; Murray & Wojciulik, 2004; Schoenfeld et al., 2007), with LO being specifically crucial for representing object shape (Grill-Spector, Kourtzi, & Kanwisher, 2001; Kourtzi & Kanwisher, 2000). We hypothesized that these areas have similar roles for the attentional selection of visual working memory representations, and predicted differential effects on the selection based on location and shape: Whereas TMS over SMG should affect internal spatial attention, TMS over LO should modulate internal feature-based attention. This dissociation would establish that there are distinct mechanisms of spatial and feature-based attention to mnemonic representations, increasing the flexibility of control over the contents of visual working memory.

Study IV

Studies I to III investigated the effects and underlying mechanisms of explicitly focusing attention on representations in visual working memory following the presentation of retrocues indicating some items as behaviourally more relevant than others. But under natural conditions, the relevance of parts of our visual environment is mostly determined by action intentions. It is not known, however, how action-relevance affects the short-term maintenance of visual information. Study IV investigated whether visual working memory representations are also weighted according to their potential action relevance. Here, action relevance was indicated by a spatial correspondence of representations with an action goal. Spatial attention is obligatorily coupled to an action goal (e.g., Baldauf & Deubel, 2010) and explicitly orienting attention to specific representations improves memory for the respective items (e.g., Griffin & Nobre, 2003; Studies I-III). Therefore, we hypothesized that representations of items that had been presented at the action goal location prior to action execution would benefit from the stronger attentional engagement at that location, resulting in better memory for these items, in a similar manner as when attention is explicitly directed towards representations following the presentation of retrocues..

Study IV used a dual-task paradigm consisting of a memory task and a movement task. During the retention interval of the memory task, for which participants had to memorize the orientations (Experiment 1) or colours (Experiment 2) of items, a pointing movement was performed towards one of several locations. The location of the item in the memory task that would subsequently be tested could either correspond to the location of the action goal or to an action-irrelevant location. Importantly, the memory and movement tasks were independent, meaning that all items were equally relevant for the memory task and only differed in their potential action-relevance as indicated by the spatial correspondence with the action goal. We expected better performance for test items presented at the action goal location than for items presented at action-irrelevant locations.

Experiment 1 additionally tested whether memory load would modulate an effect of action-relevance. We reasoned that action-related selective processing might become particularly important when the need for selective processing is high, that is, when memory load is increased up to the limit of visual working memory capacity (e.g., Luck & Vogel, 2013). For the perceptual domain, the deployment of attention has been shown to be spatially highly specific to the action goal (e.g., Baldauf et al., 2006), presumably to increase the efficiency of processing at that location. In Experiment 2, we investigated whether a similar specificity can also be observed at the representational level by analyzing performance for memory items presented at action-irrelevant locations as a function of their distance to the action goal (i.e., neighbouring or non-neighbouring to the action goal location). Control conditions without a movement (Experiment 1) and with a movement to a goal that never corresponded to a memory item location (Experiment 2) were included to ensure that any observed effects were indeed due to the action itself, and not due to perceptual priming resulting from the cue indicating the action goal or general, spatially unspecific components of action planning.

Study V

Study V looked at another mechanism of selective action-related processing: the intentional weighting of feature dimensions. The intention to perform an action primes feature dimensions that are relevant for that particular type of action (e.g., size and orientation for grasping actions), increasing the impact of these dimensions on perceptual processing (e.g., Memelink & Hommel, 2013). In this study, we investigated whether the influence of action intentions on the processing of feature dimensions continues after the perceptual stage. Specifically, we hypothesized that planning a particular kind of action induces a weighting of representations in visual working memory, yielding better memory for items defined by a feature coded on an action-relevant dimension.

In a dual-task paradigm consisting of a memory and a movement task, participants were to memorize items defined by size or colour while preparing either a grasping or a pointing movement. Size is a relevant feature dimension for grasping actions (Smeets & Brenner, 1999), but largely irrelevant when a pointing movement towards the centre of the item is to be performed. Accordingly, we expected better performance for items defined by size when a grasping movement was being planned than when a pointing movement was being planned. Colour, on the other hand, should be irrelevant for the preparation of a grasp, but might be used to localize the goal object and guide a pointing movement (White, Kerzel, & Gegenfurtner, 2006). However, the relevance of colour for pointing movements is not as evident as that of size for grasping, and previous studies have failed to find an effect of the intention to point on the perceptual processing of colour (Bekkering & Neggers, 2002; Hannus et al., 2005). A second but more tentative prediction was therefore that performance for items defined by colour is better during the preparation of a pointing movement than during the preparation of a grasping movement. In Experiment 1, the memory task was embedded within the movement task to test for a general effect of different action intentions on the short-term maintenance of visual information. In Experiment 2, the cue indicating the type of movement to be performed was presented during the retention interval, well after the display containing the items to be memorized. This design served to ensure that any observed weighting was introduced at the representational level in visual working memory, and not the result of perceptual enhancement at the time of encoding.

2

SUMMARIES

2.1 Study I: Weighting in visual working memory – Focused and defocused representations

Reference

Heuer, A., & Schubö, A. (2016). The focus of attention in visual working memory: Protection of focused representations and its individual variation. *PloS ONE, 11*, e0154228. doi:10.1371/journal.pone.0154228

Summary

Attention can be internally oriented towards items maintained in visual working memory, yielding improved memory for these focused items (e.g., Griffin & Nobre, 2003). Study I investigated whether the internal deployment of attention can be used to flexibly weight the contents of visual working memory according to differences in their task-relevance. Specifically, we examined whether less task-relevant and intermittently defocused items remain available in a scenario in which they might become relevant again, and, if so, if there is a cost associated with temporarily defocusing some items while continuously focusing others. In addition, we investigated whether the individual efficiency of attentional selection was related to the benefit observed for focusing task-relevant items. To address these two questions, behavioural performance and two ERP components associated with maintenance in visual working memory (CDA/SPCN) and the efficiency of attentional selection (N2pc) were analysed.

Differences in the task-relevance of specific items were established using a double-retrocue paradigm (Figure 1A). Participants were asked to memorize the colours of four items presented in the left or right visual hemifield, as indicated by a precue. The first retrocue presented during the retention interval always marked two of these items as task-relevant (Figure 1B). The second retrocue either marked the same two items (Hold condition), or it additionally marked one (Add1 condition) or two adjacent items (Add2 condition). Thus, the items indicated by the first retrocue were always task-relevant and continuously focused, but there was some likelihood that initially uncued (intermittently defocused) items would become relevant again upon presentation of the second retrocue. A neutral condition served as a baseline for when no subset of items was focused.

Figure 1C shows the main results of Study I. Performance for intermittently defocused items was well above chance level, showing that defocused items remain available when there is some likelihood that they might become task-relevant again. However, performance for these items was worse than for continuously focused items, indicating that refocusing items cannot boost them back to the initial level, but that there is a cost associated with defocusing. This cost seemed to be higher when the likelihood to become task-relevant again was lower. Importantly, performance for continuously focused items was at the same level in all conditions and was not affected by the inclusion of intermittently defocused items in the Add conditions. Thus, the most task-relevant information was robustly maintained inside the focus of attention. (No converging conclusions with respect to the first question we addressed could be drawn based on the CDA/SPCN results, because these were inconsistent with the prevailing view that this ERP component reflects the number of maintained items. Instead, our findings suggest that the CDA/SPCN is associated with the internal focus of attention. These findings and implications for the interpretation of the CDA/SPCN are discussed in more detail in the original article, see Appendix p. 59). Second, we asked whether individual attentional efficiency was related to the magnitude of the behavioural benefit of focusing task-relevant items. Indeed, stronger N2pc modulations indicating higher attentional efficiency were associated with larger retrocueing benefits. This finding adds to a growing body of literature highlighting the importance of individual attentional control for working memory functions (e.g., Fukuda & Vogel, 2009, 2011; Vogel et al., 2005).

In short, the results of Study I show that information in visual working memory can be flexibly weighted according to its relevance, presumably in different attentional states (e.g., LaRocque et al., 2014), and that individual differences in attentional efficiency contribute to how pronounced this weighting is.

2.2 Study II: Spatial and feature-based attentional selection of representations

Reference

Heuer, A., & Schubö, A. (2016) Feature-based and spatial attentional selection in visual working memory. *Memory & Cognition, 44*, 621-632. doi: 10.3758/s13421-015-0584-5

Summary

The investigation of the attentional modulation of maintenance in visual working memory has almost exclusively focused on spatial attention: Spatial retrocues were used to mark locations at which memory items had previously been presented (e.g., Griffin & Nobre, 2003). For attentional orienting to perceptual input, it has long been established that it can rely not only on spatial but also

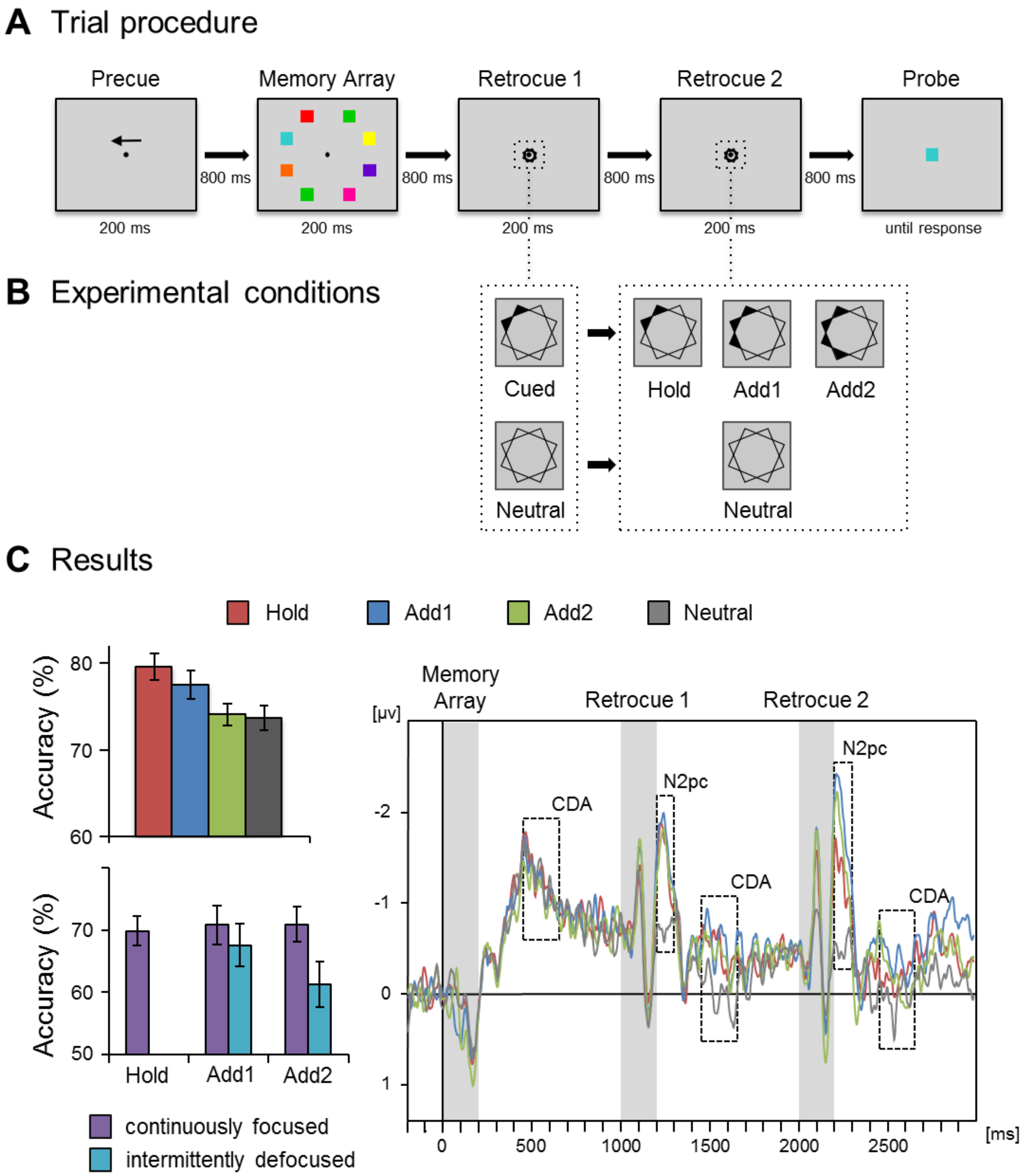

Figure 1. Study I. (A) Trial procedure. (B) Experimental conditions and examples of the retrocues used in the different conditions. (C) Results. The top left panel shows accuracy in percent for each experimental condition. The bottom left panel shows accuracy in percent for the continuously focused items and for intermittently defocused items in the Add conditions and in the Hold condition. Error bars show the standard errors of the means. The right panel shows the grand-averaged ERP difference waves (contralateral activity minus ipsilateral activity) for the experimental conditions, time-locked to the onset of the memory array, averaged across parieto-occipital electrodes (PO3/PO4, PO7/PO8). Time windows of stimulus presentations are shaded in grey. Time windows for N2pc and CDA/SPCN analyses are indicated by grey dotted squares. For illustration purposes the waveforms were lowpass filteres (half-amplitude cutoff at 35 Hz, 24 dB/oct).

on featural information, and spatial and feature-based attention have been shown to exhibit different characteristics, indicating that these are distinct mechanisms (e.g., Carrasco, 2011; Greenberg et al., 2010; Jans et al., 2010b). Study II investigated whether a similar flexibility with respect to the kind of information that can be used for attentional selection also applies to internal attention towards representations in visual working memory by testing the efficacy of different spatial and feature-based retrocues. To test whether these two types of retrocues rely on distinct attentional mechanisms, differences in access to representations of items presented at neighbouring and non-neighbouring locations were examined.

In two experiments, participants performed a visual working memory task, for which they memorized the orientations (Experiment 1; Figure 2A, top row) or colours (Experiment 2; Figure 2A, bottom row) of four items in the left or right visual hemifield, as indicated by a precue. The task was lateralized to allow for the presentation of items spaced closely enough to be considered as neighbouring or non-neighbouring without exceeding visual working memory capacity. During the retention interval, a valid retrocue indicating two memory items was presented. This was either a typical spatial retrocue (an octagram with blackened corners pointing to two locations), a symbolic spatial retrocue (numbers mapping onto two locations) or a feature based retrocue: a colour retrocue (a blob of the colour of two items) in Experiment 1 and a shape retrocue (an outline of the shape of two items) in Experiment 2. The two cued items had been presented at either neighbouring or non-neighbouring locations. A neutral retrocue condition was used as a baseline for when no subset of items was selected. At the end of each trial, participants were to judge whether the test item was of the same orientation (Experiment 1) or of the same colour (Experiment 2) as the memory item previously presented at that location.

Overall retrocueing benefits (not shown in Figure 2) in terms of both higher accuracy and faster reaction times as compared to a neutral retrocue condition were observed for all retrocue types. Whereas feature-based retrocues were effective for both neighbouring as well as non-neighbouring cued items, spatial retrocues only yielded benefits for cued items presented at neighbouring locations (Figure 2B).

These findings demonstrate that attentional selection of representations in visual working memory can operate on different visual properties that carry information about the relevance of specific items, increasing the flexibility of visual working memory updating. Importantly, moreover, the observation that spatial and feature-based retrocues differ with respect to access to representations of items presented at neighbouring and non-neighbouring locations suggests that there are distinct mechanisms for spatial and feature-based attention in visual working memory, similar to what is known about external attention to perceptual input.

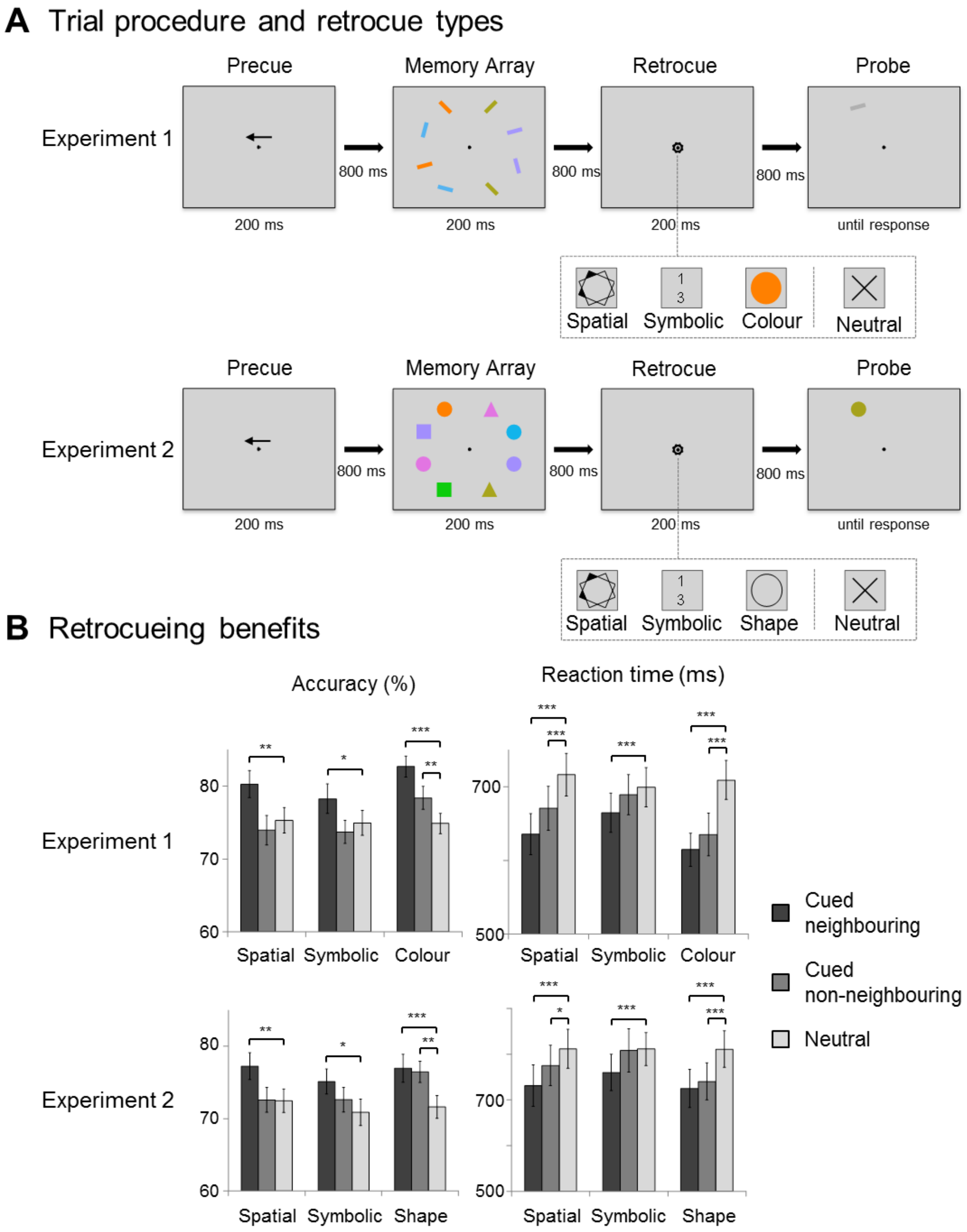

Figure 2. Study II. (A) Trial procedure and retrocue types of Experiment 1 (top) and Experiment 2 (bottom). Participants were to remember the four orientations (Exp. 1) or colours (Exp. 2) in the hemifield indicated by the precue. (B) Retrocueing benefits for neighbouring and non-neighbouring items in Experiment 1 (top) and Experiment 2 (bottom). The left panel shows accuracy in percent, the right panel shows mean reaction times, separately for the three different retrocue types. Error bars show the standard errors of the means, and asterisks mark significant retrocueing benefits (i.e., significant differences between informative and neutral retrocues). * $p < .05$; ** $p < .01$; *** $p < .001$

2.3 Study III: Cortical dissociation of spatial and feature-based attention

Reference

Heuer, A., Schubö, A., & Crawford, J. D. (submitted). Different cortical mechanisms for spatial vs. feature-based attentional selection in visual working memory.

Summary

Study II provided behavioural evidence that there are distinct mechanisms for spatial and feature-based attentional selection of visual working memory representations. Building on these findings, Study III sought to further corroborate this notion by dissociating spatial and feature-based attention at the cortical level using transcranial magnetic stimulation (TMS). To do so, we again drew on what is known about external attention: Largely overlapping networks of frontal, parietal and occipital regions are involved in both spatial and feature-based attention, but subregions or populations of neurons within these networks have been shown to be specific or preferential for one of these two mechanisms (Giesbrecht et al., 2003; Greenberg et al., 2010; Schenkluhn et al., 2008; Slagter et al., 2007; Vandenberghe et al., 2001). The aim of Study III was to identify regions that are specific for either spatial or feature-based attention in visual working memory.

The task (Figure 3A) was similar to the one used in Study II. Participants memorized the colours of three differently shaped items presented in the left or right visual hemifield. During the retention interval, a retrocue was presented that was either spatial (an arrow pointing to one location) or feature-based (an outline of the shape of one of the items). These two types of informative (cued) retrocues varied blockwise and were interleaved with neutral retrocues (see Figure 3B). Starting 100 ms after retrocue onset, three pulses of TMS were applied over either the right supramarginal gyrus (SMG), which has been shown to be involved in external spatial attention (Chambers et al., 2004; Schenkluhn et al., 2008), or the right lateral occipital cortex, which is involved in external attentional selection based on shape (e.g., Grill-Spector et al., 2001; Murray & Wojciulik, 2004; Schoenfeld et al., 2007) (Figure 3C). Upon presentation of the test item, participants were then to indicate whether the colour of this item was the same as that of the memory item previously presented at that location.

We found that TMS over SMG selectively facilitated performance for spatial retrocues, whereas TMS over LO selectively facilitated performance for shape retrocues (Figure 3D). Importantly, this pattern was observed in cued trials but not in neutral trials, in which no attentional selection was required. Moreover, the double dissociation was only observed for items in the visual hemifield contralateral to the stimulation sites. This is likely due to the nature of the representations attention operates on when selecting information in visual working memory, for which hemispheric lateralization has been demonstrated (e.g., Gratton, 1998; Vogel & Machizawa, 2004), and it is

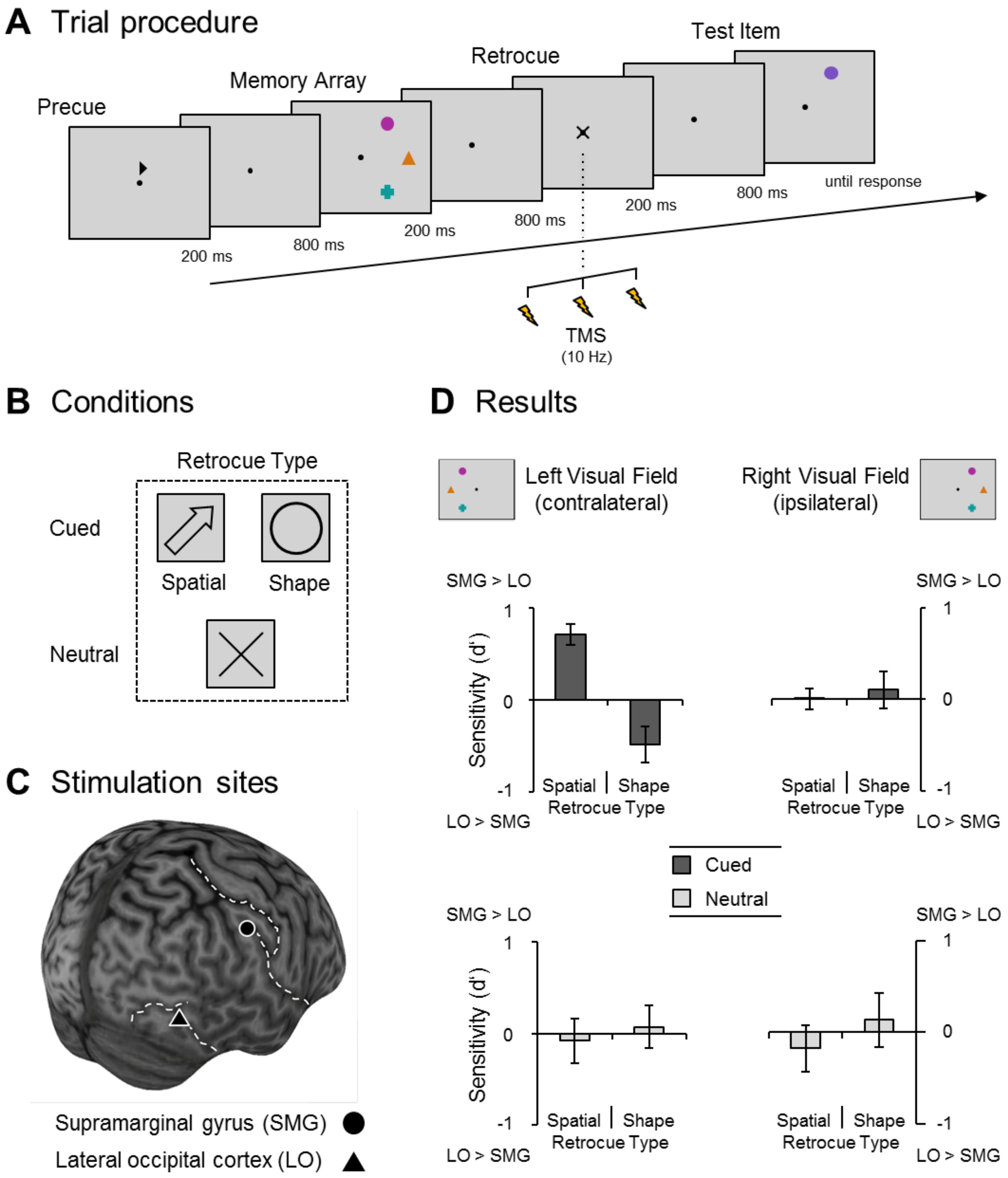

Figure 3. Study III. (A) Trial procedure. Participants memorized the colours of the items in the memory array. In TMS conditions, a train of three pulses was applied during and following retrocue presentation. The first pulse was delivered 100 ms after retrocue onset. (B) Conditions and examples of retrocue types. (C) Location of TMS sites SMG and LO in the right hemisphere of one participant. Dashed lines indicate the sulci used to identify the sites. (D) Results. Shown are the differential effects (SMG minus LO) in the sensitivity of change detection (*d'*) relative to the no-TMS baseline, separately for left- and right-hemifield trials and for cued (dark grey, top row) and neutral trials (light grey, bottom row). Positive values indicate improved performance with TMS to SMG, negative values indicate improved performance with TMS to LO. Error bars show the standard errors of the means.

consistent with electrophysiological findings of lateralized activity following retrocues (Griffin & Nobre, 2003; Myers, Walther, Wallis, Stokes, & Nobre, 2015; Poch et al., 2014; Study I).

In sum, Study III showed that different cortical areas subserve spatial and feature-based selection in visual working memory, substantiating the notion of distinct attentional mechanisms. Seeing as the same areas have been implicated in the control of external attention based on spatial and featural information, the results further indicate that these attentional mechanisms are similarly implemented in parietal and occipital cortex.

2.4 Study IV: Action-induced weighting of representations

Reference

Heuer, A., Crawford, J. D., & Schubö, A. (submitted). Action-relevance induces an attentional weighting of representations in visual working memory.

Summary

Study IV investigated whether representations in visual working memory are also weighted according to differences in their potential action-relevance, as indicated by a spatial correspondence with the action goal location. As spatial attention has been shown to be coupled to an action goal (e.g., Baldauf & Deubel, 2010), we hypothesized that representations of items previously presented at the action goal location would benefit from the action-related deployment of attention to that location, yielding improved memory for these items.

In a dual-task paradigm, participants memorized the orientations (Experiment 1) or colours (Experiment 2; Figure 4A) of items and performed a pointing movement during the retention interval. Pointing movements were performed towards a glass plate placed in front of the monitor (Figure 4B). The test item in the memory task was presented at a location that either corresponded to the goal of the pointing movement, or at an action-irrelevant location. In control conditions, participants performed either no movement following the cue that otherwise served to indicate the movement goal (Experiment 1) or a movement towards a goal that never corresponded to a memory item location, the fixation dot (Experiment 2; Figure 4A).

Indeed, performance for test items presented at a location corresponding to the action goal was better than for test items presented at action-irrelevant locations (Results of Experiment 2 are shown in Figure 4D). Varying the number of memory items (the set size) in Experiment 1 further revealed that this effect was sensitive to memory load, indicating that preferential maintenance of potentially action-relevant items becomes particularly evident when the demand on visual working memory is high. We propose that this weighting of maintained items according to their potential

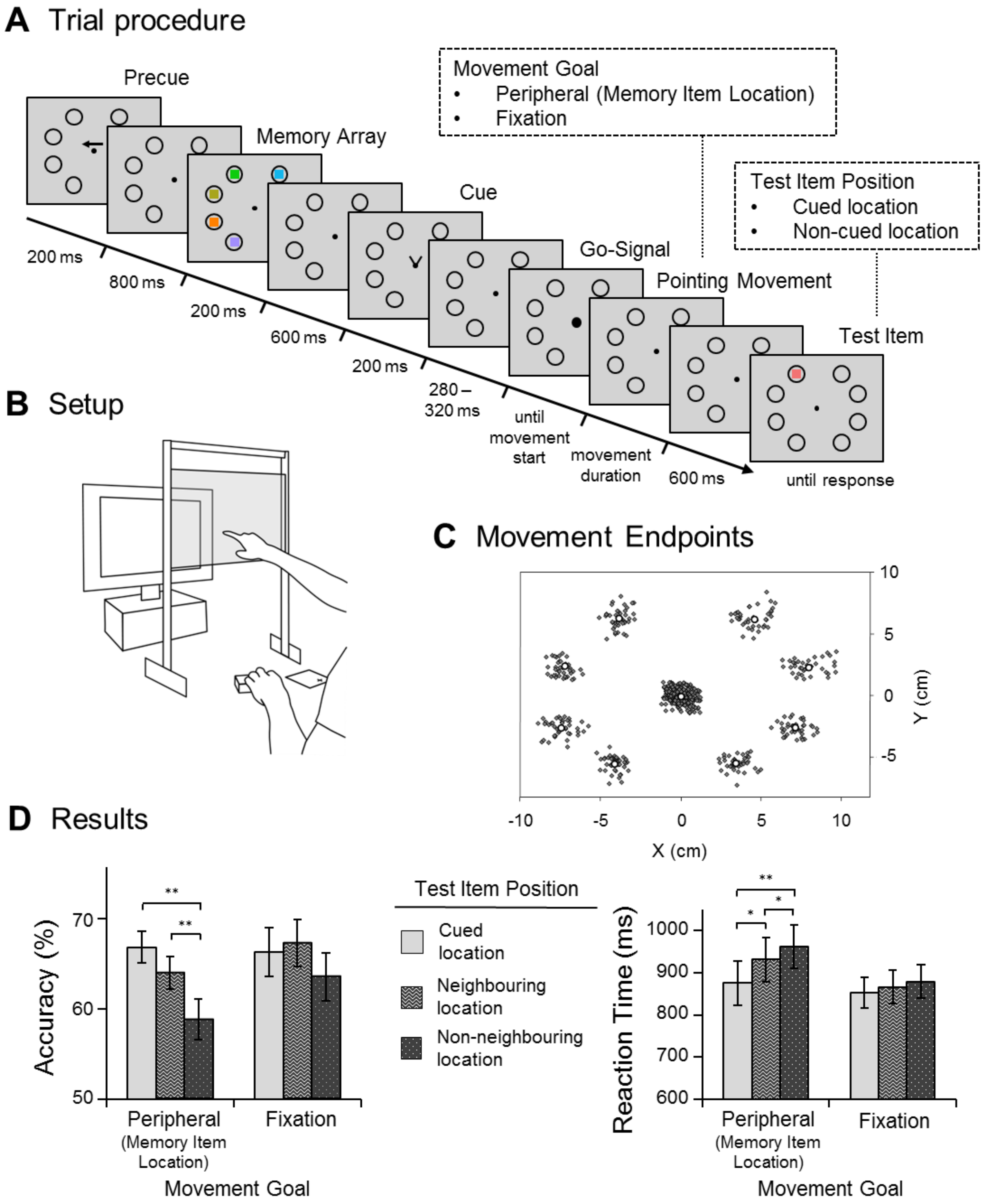

Figure 4. Study IV. (A) Trial procedure of Experiment 2. Participants were to perform a pointing movement towards either the peripheral memory item location indicated by the cue or to the fixation dot. In 25% of all trials, the test item was presented at the cued location, in 75% it was presented at a non-cued location. (B) Experimental setup. (C) Movement endpoints of a single participant in Experiment 2. Circles show the mean endpoints of the different movement goals. (D) Results of Experiment 2. The left panel shows accuracy in percent, the right panel shows mean reaction times, separately for the different test item positions and movement goals. Asterisks mark significant differences (* $p < .05$; ** $p < .01$). Error bars show the standard errors of the means.

action relevance is mediated by the deployment of spatial attention to the action goal, which benefits representations spatially corresponding to that location. Performance was still better at locations next to the action goal than at locations farther away (Experiment 2; Figure 4D), suggesting that, at the representational level, the effect of the deployment of attention to the action goal location is spatially not specific to that location, but that there is an attentional gradient spreading out from the action goal.

The results of Study IV demonstrate that our actions continue to influence visual processing beyond the perceptual stage during working memory maintenance. Thus, the contents of visual working memory cannot only be modulated by explicitly focusing attention on certain representations, but an action-related automatic deployment of attention also induces a corresponding weighting of representations according to their potential action-relevance.

2.5 Study V: Selective weighting of action-relevant feature dimensions

Reference

Heuer, A., & Schubö, A. (submitted). Selective weighting of action-related feature dimensions in visual working memory.

Summary

Planning an action primes feature dimensions that are relevant for that particular action, increasing the impact of these feature dimensions on perceptual processing, which ensures the availability of visual information necessary for parameter specification and online action control (e.g., Memelink & Hommel, 2013). Study V combined a movement task with a visual working memory task to test whether this mechanism of selective action-related processing also affects the short-term maintenance of visual information.

The trial procedures of Study V are shown in Figure 5A. For the memory task, participants memorized four items in each trial, two defined by size and two defined by colour. After a retention interval, a test item was presented, which was defined by the same feature dimension as the item that had previously been presented at that location, and participants were to indicate whether there was a change in size or colour, respectively (Figure 5C). For the movement task, a cue depicting either a grasping or a pointing movement was presented (Figure 5B), and participants were instructed to prepare the respective movement but to withhold execution until after completion of the memory task. Size is a relevant feature dimension for grasping movements (Smeets & Brenner, 1999) but largely irrelevant for pointing movements. Colour, in contrast, should be irrelevant for planning a grasping movement, but might be used to localize the action goal and to guide a pointing movement

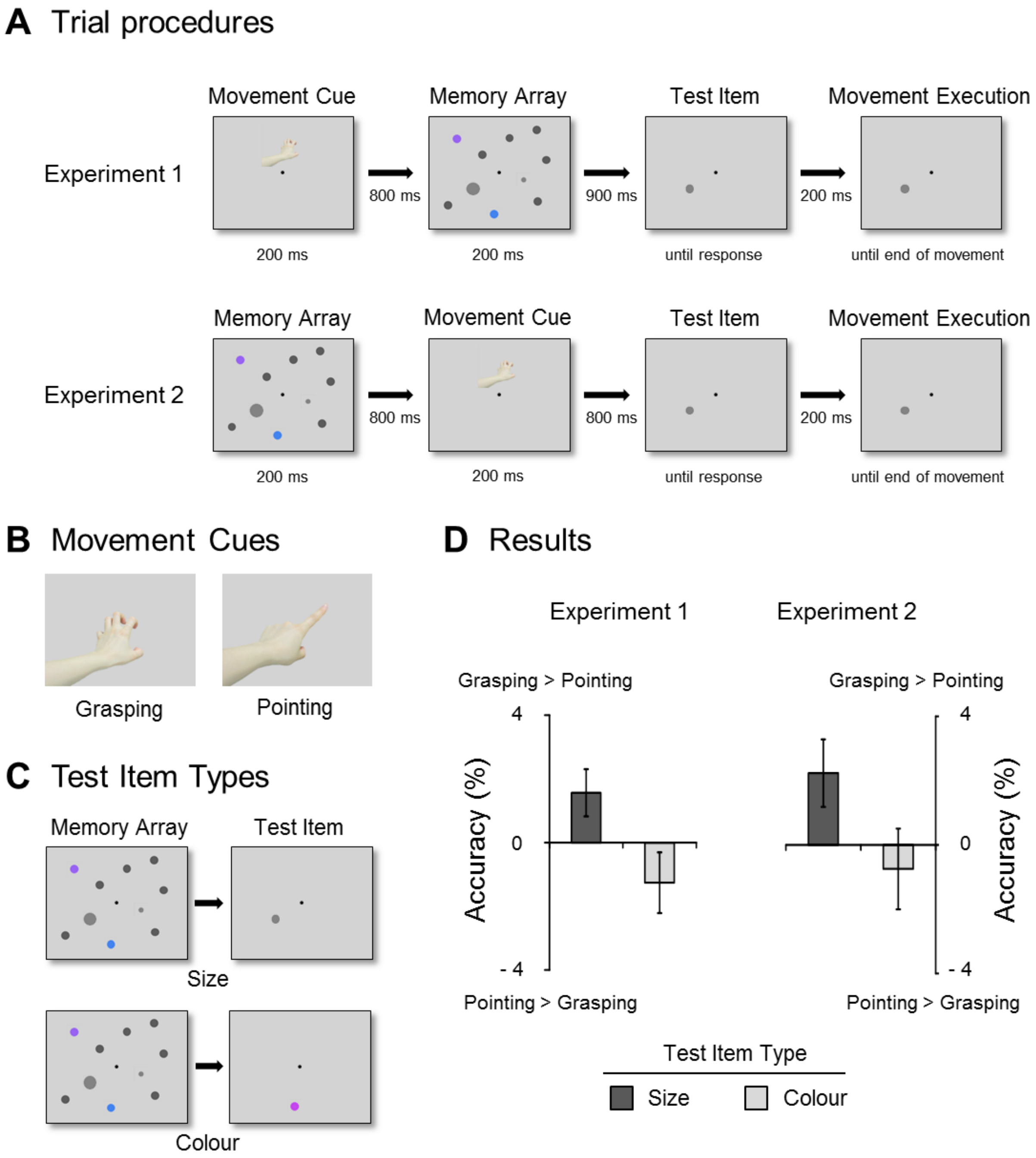

Figure 5. Study V. (A) Trial procedures of Experiment 1 (top) and Experiment 2 (bottom). Participants were instructed to memorize the two colours and the two sizes of the deviating items in the memory array. (B) Movement cues for grasping (left) and pointing movements (right). (C) Examples of the memory task for a size test item (top) and for a colour test item (bottom). (D) Results of Experiment 1 (left) and Experiment 2 (right). Shown are the differences in accuracy in grasping movement and pointing movement trials (grasping minus pointing), separately for size test items (dark grey) and colour test items (light grey). Positive values indicate better performance during the preparation of a grasping movement, and negative values indicate better performance during the preparation of a pointing movement. Error bars show the standard errors of the means.

(White et al., 2006). Accordingly, we expected better performance for size items during the preparation of a grasping movement than during the preparation of a pointing movement, and better performance for colour items when a pointing movement was being planned than when a grasping movement was being planned. In Experiment 1, the memory task was embedded in the movement task, that is, the movement cue was shown prior to the presentation of the items to be memorized. In Experiment 2, the movement cue was presented during the retention interval.

Indeed, memory for items defined by size was better during the preparation of a grasping movement than during the preparation of a pointing movement (Figure 5D). Conversely, memory for colour tended to be better when a pointing movement was being planned than when a grasping action was being planned. However, the effect of action intention on performance for colour items was weaker and failed to reach significance. In Experiment 1, the movement was already being prepared when the to-be-memorized items were presented, and the effect of action intention can accordingly be interpreted as the result of perceptual enhancement of action-related feature-dimensions at encoding. Importantly, the same effect was observed in Experiment 2, in which the movement to be performed was only instructed during the retention interval. This demonstrates that a selective action-related weighting of items can also be introduced at the representational level during visual working memory maintenance.

In sum, the results of Study V revealed that action-relevant feature dimensions are not only selectively enhanced during perception, but also preferentially maintained in visual working memory, ensuring the availability of necessary information for upcoming actions.

3

GENERAL DISCUSSION

In five studies, this dissertation project examined how the contents of visual working memory can be flexibly updated and weighted to reflect differences and changes in their relevance for current behavioural goals. At a broad level, the dissertation can be regarded as consisting of two parts.

The first part (Studies I – III) investigated how this updating is accomplished when retrocues presented during the retention interval indicate some maintained information as more task-relevant than other, inducing an explicit and strategic allocation of attention to the respective representations. Results showed that this attentional selection of representations yields a benefit (i.e., better memory) for task-relevant information (Studies I – III), with the magnitude of this benefit being related to the attentional efficiency of an individual (Study I). The consequence of this attentional selection for the other, unselected representations is sensitive to task context: When there are graded differences in the relevance of maintained information, the contents of visual working memory can be weighted to reflect these differences. While the most important information is robustly maintained inside the focus of attention, less important information can be maintained in a more vulnerable state outside the focus of attention, from where it can be accessed to be refocused and retrieved if need be (Study I). Studies II and III established that different visual properties (e.g., location or colour) can be used to guide the selection of relevant representations. A basic distinction can be drawn between mechanisms of spatial and feature-based attentional selection, which can be dissociated in terms of behavioural signatures (Study II) and involved cortical areas (Study III).

The second part (Studies IV and V) focused on more natural and implicit indicators of the relevance of specific aspects of our visual surroundings, namely actions and action intentions. The results revealed that selective action-related processing continues to influence visual processing beyond the perceptual stage, inducing an updating of visual working memory that reflects differences in the action-relevance of representations. Representations that hold potential action-relevance because they spatially correspond to the location of an action goal (Study IV) or because they contain information that is coded on a feature-dimension that is critical for a particular type of action being prepared (Study V) are preferentially maintained and recalled with higher accuracy than information that is action-irrelevant. This relative enhancement of action-related representations ensures that any information that may be required for action planning and control is readily available. Prioritized maintenance of action-relevant information should consequently be particularly important when the demand on visual working memory is high. Indeed, the effect of actions on maintenance was found to be particularly pronounced when memory load corresponded to the average visual working memory capacity (Study IV). Furthermore, Study IV provided evidence that action-related enhancement at the mnemonic level is spatially not as precise to an action goal as it has been shown to be for perception (e.g., Baldauf et al., 2006). Instead, results indicated a graded enhancement spreading out from the representation corresponding to the action goal location.

There is one difference between the updating of visual working memory following retrocues in the first part of this dissertation and the updating following actions or action intentions in the second part that should be noted. In the first part (Studies I – III), this updating in terms of a weighting of representations reflected differences in the relative *task-relevance* in a memory task. The second part (Studies IV and V) used dual-task paradigms: actions manipulated the relative *action-relevance* of maintained items, while their *task-relevance* for a concurrent memory task was unaffected and equivalent.[1] Here, updating was required to reflect differences in the *action-relevance* of items in order to protect particularly important information, without overly impairing the maintenance of less *action*-, but still *task-relevant* information. Thus, relevance for both tasks needed to be considered. Updating of visual working memory is sensitive to task context (Study I; Gunseli, van Moorselaar, Meeter, & Olivers, 2015; Zokaei, Ning, Manohar, Feredoes, & Husain, 2014), and it is likely that the implemented weighting in Studies IV and V was accordingly less pronounced than in Studies I to III. For one, this may be the reason why the overall effects (i.e., differences in performance for more and less relevant information as indicated by retrocues or actions) were smaller in Studies IV and V. More importantly, this means that these studies might underestimate the effect that actions can have on the short-term maintenance of visual information under truly natural conditions (i.e., when there is no concurrent memory task to be performed).

Drawing on research on selective action-related *perceptual* processing (e.g., Baldauf & Deubel, 2010; Memelink & Hommel, 2013), one can assume that the action-related modulation of *mnemonic* processing as observed here is mediated by an automatic and obligatory (internal) allocation of attention, enhancing the processing of information represented at action-relevant “internal locations” or in action-relevant feature dimensions throughout the spatial layout of visual working memory. The roles of attention and action in the updating of visual working memory should consequently be considered joint, and the two parts of this dissertation are by no means separate,

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[1] Note that this was purposely done to isolate the effect of the action. If the action affected the relevance of items for the memory task, it would essentially be another kind of cue and most likely induce a strategic allocation of attention. Therefore, such a design would not allow for any conclusion as to whether action planning per se involves the (automatic and involuntary) preferential maintenance of action-relevant information.

but intrinsically linked. The contents of visual working memory can be weighted to reflect differences in their relevance, irrespective of whether this relevance is explicitly indicated by external cues or more implicitly indicated by action intentions of an agent. This already points to what is the common thread running through the results of all five studies: updating of visual working memory is remarkably *flexible*.

3.1 Flexibility of visual working memory updating

3.1.1 …with regard to context and the *relative* relevance of representations.

All studies of this dissertation project were based on and further corroborated the idea that even when all representations were created equal (i.e., were equally relevant at encoding), they do not necessarily remain so during maintenance: When some representations are more important than others, they can be attentionally selected, resulting in better memory for the respective information. As outlined above, the consequences of this selective updating for unselected representations are not yet well understood. Study I addressed this question and showed that updating of visual working memory does not follow an all-or-nothing principle in that relevant representations are attentionally selected and maintained while all other contents are consequently considered irrelevant and discarded. Instead, attention can be used to establish different representational states (LaRocque et al., 2014) that allow for a weighting of visual working memory contents that reflects graded differences in their relevance for current goals.

Maintenance of the most important information inside the focus of attention renders this information particularly robust. It has previously been shown that representations in the focus of attention are protected from decay and less susceptible to interference from novel stimuli or other representations (e.g., Landman et al., 2003; Makovski & Jiang, 2007; Makovski et al., 2008; Matsukura et al., 2007; Sligte et al., 2008, 2010). The results of Study I extended these findings by demonstrating that maintenance of focused representations is even unaffected by the inclusion of additional representations into the focus of attention: Performance for the continuously focused items in the Add conditions, in which one (Add1) or two (Add2) items were "added" to the focus of attention after the second retrocue, was equivalent to performance for the continuously focused items in the Hold condition, in which only these items were maintained in the focus of attention.

Information that is less relevant for the task at hand can be kept available in a more fragile, defocused state, and thus refocused and retrieved at a later point in time, when or if it is needed. Thus, defocusing representations does not necessarily lead to their loss, but maintenance outside the focus of attention does appear to come at a cost: While memory for the intermittently defocused items in the Add conditions was well above chance level, it was worse than for continuously focused items. Maintenance outside the focus of attention might even hold the potential to reflect differences in relevance at a more fine-grained level. In the Add1 condition, the likelihood for the intermittently defocused item to become task-relevant again upon presentation of the second retrocue was somewhat larger than for the intermittently defocused items in the Add2 condition. Consistent with this difference in relevance, performance for intermittently focused items was better in the Add1 condition than in the Add2 condition.

These findings converge with those of recent studies that manipulated retrocue reliability and observed that the fate of defocused items critically depended on their relevance to the task. Zokaei, Ning, Manohar, Feredoes, and Husain (2014) found that defocused items can later be brought back into the focus of attention and recalled as long as they remain behaviourally relevant, but that items that are very unlikely to be tested (i.e., in only 20% of all trials), are lost. Gunseli, van Moorselaar, Meeter, and Olivers (2015) observed both greater benefits of valid retrocues as well as greater costs of invalid retrocues when cue reliability was high compared to when it was low. Taken together with studies showing that information *can* be removed from memory when it is reliably rendered irrelevant by a cue (Williams et al., 2013; Williams & Woodman, 2012), these findings and the results of Study I indicate a high sensitivity of visual working memory to the relative relevance of memoranda in a specific task context. Memory contents can be modulated to reflect the probability structure of that task context by adopting different representational states that can be flexibly adjusted and switched during maintenance (van Moorselaar, Olivers, Theeuwes, Lamme, & Sligte, 2015). This adaptability of updating ensures an optimal use of the limited capacity of visual working memory in a given situation: Particularly important information is robustly maintained inside the focus of attention, currently less important information that might still be useful to have available in the future can be maintained outside the focus of attention (and conceivably with different degrees of robustness), and irrelevant information can be excluded, thereby freeing capacity for new input.

How the weighting of visual working memory contents in terms of different representational states might be implemented at the neural level is yet not fully understood. Whereas maintenance inside the focus of attention is mostly considered to be based on feedback connections with frontal and parietal areas, modulating sustained neural firing (e.g., LaRocque et al., 2014; van Moorselaar et al., 2015), maintenance outside the focus of attention remains more of a mystery and several possible mechanisms have been suggested, for instance recurrent loops in and with parietal areas (van Moorselaar et al., 2015) or temporarily modified connection strengths (Olivers et al., 2011). This is not just an interesting question in itself, but also important to clarify whether the distinction between maintenance inside and outside the focus of attention is merely a useful descriptive concept or whether it reflects qualitatively different forms of maintenance. The most compelling piece of evidence that maintenance within and outside the focus of attention are indeed not only quantitatively different (e.g., more or less neural firing, stronger or weaker connections between prefrontal areas and parietal or occipital areas), but qualitatively distinct was provided by Lewis-Peacock et al. (2012) and LaRocque et al. (2013). Using multivariate pattern analysis of fMRI and EEG data, these studies found evidence for elevated neural activity during the delay period only for information maintained in the focus of attention, but not for other (uncued) information that could nevertheless be retrieved and was thus clearly maintained in some way. The authors point out that the long-standing notion that the short-term retention of information is accomplished by sustained neural delay activity (e.g., Curtis & D'Esposito, 2003; Fuster & Alexander, 1971; Miller, Li, & Desimone, 1993; Vogel & Machizawa, 2004; for an overview see McCollough et al., 2007) is based on studies in which memory and attention were confounded: all items to be memorized were (equally) task-relevant throughout the retention interval and therefore presumably also attended. They propose that sustained, elevated neural firing reflects maintenance inside the focus of attention, but that it is not required for the short-term retention of information per se. Whereas maintenance inside the focus of attention is activity-based, maintenance outside the focus of attention may be accomplished via weight-based mechanisms relying on synaptic modifications such as short-term potentiation (see also LaRocque et al., 2014).

3.1.2 …with regard to the representational characteristics that can guide attentional selection

Different visual properties can provide information about the (relative) relevance of certain parts of our visual surroundings, and ideally, the visual system should be able to use all of these not only for selective processing at the perceptual stage, but also for a selective weighting of the internal representations of our surroundings in working memory. Flexibility with respect to the visual characteristics that can guide selective processing has long been known to exist for external attention (e.g., Carrasco, 2011; Maunsell & Treue, 2006; Schenkluhn et al., 2008), and the present dissertation established that internal attention in visual working memory can just as well flexibly rely on different representational characteristics. Results revealed that a weighting of memory contents can be implemented when some representations are more important than others because they correspond to relevant locations (Studies I – IV) or because they contain a relevant feature (Studies II, III and V). A feature can guide the attentional selection of representations both when it is deemed more relevant than other features of the same dimension (e.g., blue is more important than green; Studies II and III), and when it is coded on a feature dimension that is more relevant than other feature dimensions (e.g., size is more important than colour; Study V). Even symbolic information (numbers mapping onto locations) can be used to guide the selection of representations (Study II). Consistent with what has been shown for external attention (Olk, Tsankova, Petca, & Wilhelm, 2014; Ristic & Kingstone, 2006), the benefits observed for symbolic retrocues were smaller than those for retrocues providing direct spatial or featural information. It seems reasonable to assume that symbolic retrocues require more time or effort to be decoded, and that this is also the reason why a previous study providing participants with less training and less time to make use of the retrocue (i.e., less time between retrocue and test item) failed to observe a benefit (Berryhill et al., 2012).

To illustrate the implications of these findings, let us go back to the example introduced above (section 1.1.2). You are picking up a friend at the station, and while you are moving your eyes to scan the area, you do not only rely on immediate visual input, but also on the representations of what you have just seen. Doing this, your visual system uses all the useful information you have: she said she would wait by the main entrance, and you expect her to wear her green jacket. Processing of representations corresponding to that location is enhanced. At the same time, green objects are preferentially processed and maintained throughout the visual field and the spatial layout of visual working memory. This renders your search most efficient: you will easily find your friend if she is indeed waiting where and wearing what you expected, but also if she is waiting somewhere else (- green objects anywhere are preferentially processed) or wearing something else (- enhanced processing of the main entrance area will help you).

A potential concern with regard to feature-based selection of representations is that the featural information might only be used to retrieve the stored information about an object's location, essentially recoding featural into spatial information. The selection of representations could then make use of the same spatial attentional mechanism that would be directly applied when spatial information is available (Pertzov et al., 2013). Such a 'detour' would obviously not be a very efficient strategy. For external attention it has been shown that there are distinct mechanisms for spatial and feature-based selection (e.g., Carrasco, 2011; Jans et al., 2010b; Maunsell & Treue, 2006). Drawing on known differences between external spatial and feature-based attention, the present dissertation established that there are analogous mechanisms of internal spatial and feature-based attention by dissociating these two types of selective internal attention behaviourally (Study II) and cortically (Study III). At the behavioural level, providing spatial information about the higher importance of some maintained items only yielded benefits when these items had been presented at contiguous locations, whereas providing featural information yielded benefits for items presented at both contiguous as well as non-contiguous locations. Similar to external attention, internal feature-based selection appears to operate in a global fashion, enhancing representations throughout the spatial layout of visual working memory, whereas internal spatial selection of non-contiguous representations seems to be harder (or even impossible) to accomplish, failing to result in detectable behavioural benefits. Study III corroborated the notion of distinct attentional mechanisms by demonstrating that different cortical regions are selectively involved in either spatial or feature-based attention: Whereas TMS to SMG selectively facilitated performance with spatial retrocues, TMS to LO selectively facilitated performance with feature-based (shape) retrocues. Taken together, the results of Studies II and III provide strong evidence that retrocues using featural information are not recoded into spatial terms, but that they rely on a distinct feature-based attentional mechanism that operates independently of spatial attention.

3.2 Selection for memory and selection for action

The two parts of this dissertation project (Studies I-III and Studies IV-V) used different means to indicate the relative relevance of maintained information (retrocues and actions), Different indicators of relevance imply that a weighting of representations was implemented for different purposes. In Studies I to III, retrocues directly manipulated the relative *task-relevance* in a memory task, and weighting maintained items accordingly served purely memory-related purposes, namely to optimize recognition performance. In Studies IV and V, actions manipulated the relative *action-relevance* of maintained items, and weighting items served to ensure the availability of information required to perform the respective actions. The ultimate purpose of any weighting in this situation was not improved maintenance per se, but a potential action-related use of the maintained information. Based on the often used distinction between selection-for-perception and selection-for-action (Allport, 1987; see also Neumann, 1987 and Goodale & Milner, 1992), one could refer to the purpose of visual working memory updating as "selection for memory" in Studies I to III, and as "selection for action" (at the mnemonic level) in Studies IV and V.

The basic mechanism enabling a weighting of representations according to differences in relevance is presumably the same in "selection for memory" and "selection for action": Internally allocating attention establishes different representational states, protecting particularly important pieces of information at the expense of others. However, it is conceivable that the different purposes of internal attentional selection imply different functional characteristics. One such characteristic that might be dependent on the purpose of attentional selection is the ability to divide the spatial internal focus of attention. As outlined above, it remains controversial whether spatial attention can be split and directed to several separate locations (e.g., Eimer & Grubert, 2014; Jans et al., 2010b), but what this ongoing debate clearly demonstrates is that this is not easily accomplished, and potentially restricted to certain conditions. A condition under which a split of external spatial attention has been repeatedly observed is during the preparation of goal-directed movements involving multiple goal locations (for an overview see Baldauf & Deubel, 2010), for instance for sequences of saccades (Baldauf & Deubel, 2008a) or pointing movements (Baldauf & Deubel, 2009), and for bimanual pointing movements (Baldauf & Deubel, 2008b). In these studies, perceptual performance was found to be facilitated at all goal locations prior to movement execution, while performance at locations in between movement goals was at chance level. This pattern of perceptual performance indicates that there were distinct foci of attention. It is thus possible that spatial attention is dividable when its purpose is to provide the information necessary for spatially accurate movements towards multiple locations (see also Baldauf et al., 2006). If the purpose of attentional selection is the critical factor here, then this should also apply to internal attention. Whereas a spatial retrocue indicating non-contiguous items as relevant for purely memory-related purposes failed to result in the preferential maintenance of several non-contiguous representations (Study II), such a split of the internal spatial focus of attention might accordingly be possible when non-contiguous representations are indicated as *action-relevant*.

Due to the general aim of this dissertation, it focused more on what is common to “selection for memory” and “selection for action” at the mnemonic level: an updating of visual working memory contents can be flexibly induced irrespective of whether differences in relevance are explicitly indicated by retrocues or more implicitly by actions. But while the result (better memory for more important information) and the basic underlying mechanism (attentional protection of some representations at the expense of others) may be the same, the example above should illustrate that there may still be notable differences depending on the purpose of this updating.

3.3 Contributions to related issues

3.3.1 The overlap of external and internal attention

From its very beginning (see Griffin & Nobre, 2003), the investigation of the allocation of attention towards representations in visual working memory has drawn on what is already known about attention to external events (Carrasco, 2011). As outlined above, this research has shown that while there are some notable differences (Nobre et al., 2004; Tanoue & Berryhill, 2012; Tanoue et al., 2013), there is also a substantial overlap of internal and external attention in terms of behavioural consequences and the underlying neural networks (e.g., Dell’Acqua et al., 2010; Griffin & Nobre, 2003; Nobre et al., 2004). The present dissertation has contributed to our knowledge about this overlap in several ways.

First, internal attention can also be flexibly guided by different stimulus characteristics (see section 3.1.2) such as location (Studies I – IV), nonspatial features (Studies II and III) or entire feature dimensions (Study V). Second, and on a related note, a basic distinction can be drawn between internal spatial and feature-based attention, as has been established for external attention. These two types of selective attention appear to operate in a similar manner over perceptual input and mnemonic representations: Whereas external and internal feature-based attention operate globally, enhancing processing of relevant information throughout the visual field or the spatial layout of visual working memory, external and internal spatial attention cannot be as easily divided among noncontiguous locations. External and internal spatial and feature-based attention also seem to be similarly implemented in parietal and occipital cortex: Study III showed that two regions that have been implicated in external attentional orienting based on location and shape (e.g., Chambers et al., 2004; Murray & Wojciulik, 2004; Schenkluhn et al., 2008) are also selectively involved in internal attentional orienting based on either stimulus characteristic. Notably, differences in the neural networks underpinning external and internal attention have mostly been observed in frontal areas (Nobre et al., 2004; Tanoue et al., 2013). Thus, one may speculate that the ability to differentiate between attention in the domains of perception and working memory is based on differential involvement of certain regions in frontal cortex, while the attentional selection and enhancement of specific properties of perceptual or mmemonic representations relies on shared circuitry in more posterior regions. The latter would be in line with accumulating evidence highlighting the similarities in neural activity associated with representations of physically present and memorized information (see for example Pasternak & Greenlee, 2005; Postle, 2006; Tsubomi, Fukuda, Watanabe, & Vogel, 2013).

Finally, similar to external attention, internal attention appears to be coupled to action planning, enhancing the maintenance of potentially action-relevant information (Studies IV and V). In Study IV, the spatial specificity of this enhancement with respect to the movement goal location was found to be not as high as it has been shown to be for external attention (Baldauf & Deubel, 2009). However, this may not be an inherent characteristic of internal attention per se. Instead, it could be related to a lower spatial resolution of working memory representations compared to perceptual representations, or the different spatial demands posed by the colour change detection task used in Study IV and the perceptually difficult discrimination task used by Baldauf and Deubel (2009).

3.3.2 The units of storage in visual working memory

Information is predominantly considered to be stored in visual working memory as integrated objects, consisting of a number of bound features (Luck & Vogel, 1997; Luria & Vogel, 2011; Vogel, Woodman, & Luck, 2001). Studies II and III are consistent with and support the notion of object-based storage. Participants were only instructed to memorize orientation (Study II, Experiment 1) or colour (Study II, Experiment 1; Study III), but they could use the features used for retrocueing to access and weight the respective representations, improving memory for the task-relevant feature. It has been shown that even task-irrelevant features are automatically encoded along with the task-relevant features, and that only subsequent maintenance is under voluntary control. Seeing as the features used for retrocueing were required to make use of the information about changes in the task-relevance of maintained items, it seems reasonable to assume that these features were encoded and then maintained along with the to-be-memorized feature in an object-based manner.

In recent years, alternative proposals have generated renewed interest in the representational unit of storage. For instance, Fougnie and Alvarez (2011) suggested that visual working memory is organized in more or less independent feature representations, with the degree of independence being determined by the degree of overlap in their neural coding during perception. Accordingly, storage of jointly coded features such as height and weight would be somewhat correlated, whereas the storage of colour and shape would be largely independent. The latter is hard to reconcile with the finding that the shape of an object can be used to improve memory for the colour of the same object (Study II, Experiment 2; Study III). Similar to the framework suggested by Fougnie and Alvarez (2011), Rajsic and Wilson (2014) proposed a feature-based representational architecture, in which nonspatial features are indexed by location. Such an architecture would seem to imply that a spatial code is necessary in order to access the nonspatial information that is nested within location. However, Studies II and III showed that a nonspatial feature (e.g., shape) can just as well be used to access another nonspatial feature (e.g., orientation).

It should be noted that the tasks used in Studies II and III strongly encouraged the binding and integrated storage of all available features. The binding of the to-be-memorized feature and location was required to perform the memory task, because the test item needed to be compared against the memory item previously presented at that particular location. And the additional binding with the feature used for retrocueing was required to make use of the cue. Such a task context emphasizing the binding of features might be a critical factor for object-based storage. Recent studies indicate that the unit of storage may not be fixed and stimulus-driven, but dependent on the global task-context: A context highlighting integration encourages storage as integrated objects, whereas a context highlighting individuation encourages individuated feature-based storage (Balaban & Luria, 2016; Vergauwe & Cowan, 2015). Such a context dependence of the unit of storage is not only consistent with the general notion of a very versatile and flexible visual working memory system, but could also reconcile the seemingly contradictory previous findings.

3.3.3 The capacity of the internal focus of attention

As outlined above, the idea of different representational states, particularly with respect to a distinction between maintenance within and outside an internal focus of attention, has been put forward by a number of working memory models, and has received substantial empirical support (for an overview see LaRocque et al., 2014). One critical aspect in which these models differ is the posited capacity of the internal focus of attention. The focus of attention has been conceptualized as either narrow and limited to one single item at a time (Oberauer, 2002; Olivers et al., 2011), or as broader and more flexible, being able to contain multiple items up to an approximate limit of four (Cowan et al., 2005). Evidence has been obtained in favour of both a limited single-item focus (e.g., Makovski & Jiang, 2007; Oberauer & Bialkova, 2009) and a multiple-item focus (e.g., Matsukura et al., 2007; Poch et al., 2014; Williams & Woodman, 2012), and the issue seems to be far from being settled (for a recent overview see Souza & Oberauer, 2016). What complicates matters further is that the different conclusions have been reached with very different paradigms (e.g., a change detection task as in Makovski & Jiang, 2007, or an arithmetic task as in Oberauer & Bialkova, 2009) or different variants of similar paradigms (e.g., a change detection task with simultaneous cueing as in Poch et al., 2014, or with sequential cueing as in van Moorselaar et al., 2015).

The present dissertation adds to this debate by providing further evidence that the focus of attention *can* contain several items. In Studies I and II, overall benefits were observed for retrocueing two and even three items. A particular strong piece of evidence for the idea that the internal focus of attention can encompass multiple items simultaneously was provided by the finding of different patterns of performance for neighbouring and non-neighbouring cued items with spatial and feature-based retrocues in Study II. This finding rules out several alternative explanations for benefits with retrocueing multiple items that do not necessarily require a multiple-item focus. First, such a benefit could be driven by the robust maintenance of only one of the cued items in the focus of attention. But if this were the case, the spatial configuration of the two items in Study II should not have made a difference, as it did for spatial retrocues: Whereas retrocueing neighbouring items led to a behavioural advantage, retrocueing non-neighbouring items did not. Second, a single-item focus could be rapidly shifted between two cued items. This might reduce a benefit for items spaced farther apart, as was the case for non-neighbouring items in Study II. However, this reasoning should then also apply to feature-based retrocues, which yielded benefits for both neighbouring and non-neighbouring items. Furthermore, the spatial distance between items does not seem to affect the time it takes to shift attention internally (Tanoue & Berryhill, 2012). Third, two cued items could be chunked and processed as one element. But chunking should have been possible with both feature-based as well as spatial retrocues. One might argue that feature-based retrocues facilitated chunking by highlighting the shared feature of the cued items (i.e., the same colour or shape). Still, this cannot account for the lack of any benefit for non-neighbouring cued items with spatial retrocues.

It should be noted, though, that these findings do not allow for the conclusion that the internal focus of attention can *always* grasp multiple items whenever needed. As pointed out above, the diverging conclusions with respect to this question are based on very different experimental tasks. There may very well be conditions, under which only one item at a time can be focused.

3.4 Future perspectives

This dissertation touched upon several topics that are worth further examination. Particularly the influence of actions on maintenance in visual working memory, which has never been systematically investigated before, provides potential starting points for future research. For instance, future studies could try to increase the ecological validity by having participants choose the action themselves. Even with careful instruction and training, cueing for a particular action always increases the likelihood that verbal or visual coding is more involved in action preparation than would naturally be the case, potentially resulting in a misestimation of the influence of actual action planning. It would also be interesting to see whether the rather broad gradient of spatial attention spreading out from the representation corresponding to the action goal, as observed in Study IV, is a characteristic of internal attention per se, of action-induced internal attention, or of the spatially not very demanding memory task used in that study. The first step could be to change the feature to be memorized, increasing the spatial demand (as in Baldauf & Deubel, 2009). For example, one could use harder to discriminate line orientations, as in Experiment 1 of Study IV. If a similar pattern of gradual enhancement spreading out from the action goal location is observed, one could then try to establish whether this lower spatial specificity (as compared to external attention, see Baldauf & Deubel, 2009; Carrasco, 2011) is a general characteristic of internal attention or of action-related internal attention: Using the same memory task, one could present a retrocue instead of having participants perform a movement. This retrocue would need to have a higher validity (e.g., 70%) than the movement cue in Study IV, and in invalid trials, one could then test items that were either neighbouring or non-neighbouring to the cued item. The latter idea is also an example for how to address the issue of whether different purposes of visual working memory updating, as discussed in section 3.2, go along with different functional characteristics.

Another promising line of research is the investigation of individual differences. Although there seems to be an increasing interest in the individual variability of elementary cognitive functions such as working memory (see also Vogel & Awh, 2008), hardly anything is known about individual differences with respect to the deployment of internal attention and visual working memory updating. Study I provided a first piece of evidence indicating that individual differences in attentional efficiency are related to the behavioral benefits of updating visual working memory contents. Future research could for instance examine how visual working memory updating, induced by either retrocues or actions, is related to an individual's visual working memory capacity. Individual capacity has previousy been shown to be associated with several other attentional and mnemonic functions such as selective and efficient encoding for visual working memory maintenance (Fukuda & Vogel, 2011; Shimi, Kuo, Astle, Nobre, & Scerif, 2014; Tseng et al., 2012; Vogel et al., 2005).

3.5 Conclusions

The present dissertation highlighted the very versatile nature of maintenance in visual working memory. Information can be updated and weighted according to even subtle differences in its relevance, while the most important information is robustly maintained in an internal focus of attention. This updating can flexibly rely on different visual properties to guide the attentional selection of relevant representations, with distinct and to some extent independent mechanisms for feature-based and spatial selection. Further, updating cannot only be achieved by a strategic and explicit internal allocation of attention, but also by a more automatic and implicit deployment of attention related to actions and specific action intentions. These findings extend our understanding of how the highly limited capacity of visual working memory is efficiently used in any given situation: a continuous and flexible selective modulation ensures that information is maintained in a manner reflecting its relevance for current behavioural goals.

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APPENDIX

Study I

PLOS | ONE

RESEARCH ARTICLE

The Focus of Attention in Visual Working Memory: Protection of Focused Representations and Its Individual Variation

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Abstract

Visual working memory can be modulated according to changes in the cued task relevance of maintained items. Here, we investigated the mechanisms underlying this modulation. In particular, we studied the consequences of attentional selection for selected and unselected items, and the role of individual differences in the efficiency with which attention is deployed. To this end, performance in a visual working memory task as well as the CDA/SPCN and the N2pc, ERP components associated with visual working memory and attentional processes, were analysed. Selection during the maintenance stage was manipulated by means of two successively presented retrocues providing spatial information as to which items were most likely to be tested. Results show that attentional selection serves to robustly protect relevant representations in the focus of attention while unselected representations which may become relevant again still remain available. Individuals with larger retrocueing benefits showed higher efficiency of attentional selection, as indicated by the N2pc, and showed stronger maintenance-associated activity (CDA/SPCN). The findings add to converging evidence that focused representations are protected, and highlight the flexibility of visual working memory, in which information can be weighted according its relevance.

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Introduction

Attention and working memory have for a long time been studied as distinct domains. In recent years, however, systematic investigations of their interrelations have revealed substantial overlap [1–5] with bidirectional influences [3,6]. In the present experiment, the attentional modulation of maintenance in visual working memory (VWM) is investigated. VWM is the system that allows us to maintain and manipulate visual information, thereby enabling us to interact with our immediate environment. Although, at each moment, we are flooded with visual information, our ability to retain this information is highly limited (e.g., [7,8]). As our environment and our goals are constantly changing, information permanently gains or loses relevance. A mechanism for dynamically modulating the information that is maintained in

VWM according to changes in relevance would thus be highly advantageous to make efficient use of this limited system. Recent studies have demonstrated that attention can be oriented towards memory representations, allowing for a flexible modulation of VWM content (e.g., [9–13]). Attentional orienting in the mnemonic and the perceptual domain have been shown to be highly similar with regard to behavioural benefits (and costs) and neural networks involved [10,12,14–20]. In order to selectively manipulate attentional orienting during the maintenance stage of VWM, these studies used retrocues, which were presented during a retention interval to orient attention to items previously presented at specific locations.

The mechanism underlying the benefit observed for memory items cued in this way is not yet entirely understood. What are the consequences of focusing a subset of items for this subset and for those items that are no longer focused? Previous studies attempting to answer this question can broadly be assigned to one of two theoretical accounts. They either concluded that attention serves to reduce memory load, or that attention is employed to protect focused items. Previous findings shall in the following be presented within this framework. Before that we briefly introduce some key terms as we use them here.

Focused, defocused and refocused information in VWM

The present experiment is based on the idea that there is an internal focus of attention (FoA) that implies different states of representations in VWM: within and outside this FoA (see [21–23]). There is a growing body of evidence supporting this notion [24–28]. Focused items are those items which are currently maintained and in the FoA within VWM. Defocused items have recently been focused, but have, at least intermittently, left the FoA. These items can be refocused, that is, brought back into the FoA. This terminology is based on the terminology used by Rerko and Oberauer [29], but differs with respect to the meaning of "unfocused" information. Rerko and Oberauer [29] defined "unfocused" information as "information that has not been focused (attended) after initial encoding." Our different understanding results from a different concept of the FoA. There is an ongoing debate on whether the FoA is a single-item focus (e.g., [22]) or whether it can hold more than one item. The present experiment is based on the idea of a flexible FoA, as suggested by Cowan et al. [30], according to which attention can "zoom in" on single items or "zoom out" to grasp multiple items. According to Cowan's and our understanding, several items may be initially focused, and the FoA would only then zoom in on specific items when information with respect to differences in the relevance of the maintained items becomes available, that is, after a retrocue has singled out one or several items. Following this line of reasoning, all memorized items are in the FoA after encoding, and accordingly there is no information in VWM that has never been focused after initial encoding.

Protection of focused items

One scenario for the consequences of attentional selection within VWM is that attention is employed to protect focused items, while defocused items are subject to faster decay. There are two major predictions which may be derived from this "protection account". First, memory for continuously focused items should be better than for unfocused or intermittently defocused items. Second, defocused items should remain available for recall and comparison with a probe, that is, a test stimulus. Previous studies provide some support for both predictions.

Matsukura, Luck, and Vecera [31] provided early evidence that attention is used to protect cued items from degradation, rather than prioritizing these items at recall. Murray, Nobre, Clark, Cravo, and Stokes [32] were able to show that retrocues increased the likelihood of recall, and that more items were available after retrocueing than in a no-cue condition. The authors propose that attention does not only protect items from decay, but that it can even serve to restore items which would otherwise be unavailable to retrieval mechanisms. A number of studies have shown that retrocueing renders an item more robust against interference from subsequent stimuli [33–36]. As pointed out by Pertzov, Bays, Joseph, and Husain [37], protection from degradation and enhancing robustness against interference are by no means mutually exclusive. Retrocueing may protect selected items from interference, which may either arise from novel incoming stimuli or from other items residing in memory.

As to the second prediction derived from the protection account, there is evidence that unfocused information remains available and that defocused items remain strengthened [29] with recently focused items being more easily recollected when only little time has elapsed from focusing them [38]. Poorer memory for defocused information might be due to forgetting as a function of time [29] or due to enhanced forgetting as compared to when no subset of items is focused [37], but for the purpose of the present experiment it suffices to assume that defocused items remain available, yet memory for them is worse than for continuously focused items.

Memory load reduction

Kuo et al. [11] suggested that attention may be employed to reduce memory load. They asked participants to perform a VWM task in which a retrocue was either informative or neutral. The Contralateral Delay Activity (CDA, see [39], also called Sustained Posterior Contralateral Negativity (SPCN), see [40], or Contralateral Negative Slow Wave (CNSW), see [41], and in the following referred to as CDA/SPCN), a lateralized event-related potential (ERP) component that is sensitive to the number of maintained items [39,42], revealed a larger amplitude attenuation after an informative retrocue than after a neutral one. Thus, retrocues that reduced the number of relevant items also reduced delay activity associated with the maintenance of information. The authors interpreted this finding as attentional selection in terms of a reduction of the number of items being maintained. But they did not test performance for those items rendered irrelevant by the retrocue to make sure that they were no longer being maintained.

That uncued items were never tested in the study of Kuo et al. might have been a crucial factor in determining the fate of these items. Indeed, it has been demonstrated that representations are excluded from VWM following so-called “directed-forgetting cues”, which are almost always valid [43]. In this extreme situation, when information is either relevant or absolutely irrelevant, is seems highly beneficial for an efficient use of the limited VWM system to discard any uncued items. These findings do not, however, allow for a conclusion as to whether or not the defocusing of representations necessarily leads to an exclusion of these representations. Given that a selection of relevant information already occurs for encoding into VWM [3], the situation created by valid retrocues that some of this information is absolutely irrelevant shortly thereafter during maintenance is rather unlikely to be frequently encountered outside the laboratory. A situation that might better reflect everyday life would be that some information is currently more relevant, warranting attentional protection, while other information might still be important in the future and thus worth holding on to.

Rationale of the experiment

In the present experiment, we addressed two issues. First we examined the fate of intermittently defocused items. Do they remain available in a scenario in which they may become task-relevant again? And if they do, is there a cost associated with defocusing, or does refocusing boost these items to a level similar to that of continuously focused items? Second, we investigated whether higher individual efficiency of attentional orienting within VWM was associated with a greater retrocueing benefit. In a double-retrocue paradigm, a first retrocue directed attention to two memory items. Thereafter, the FoA was either constant throughout the entire trial (Hold condition), or it had to be expanded to again include either one (Add 1 condition) or two (Add 2 condition) previously defocused items. A neutral retrocue condition provided the baseline for when no subset of representations was focused. Participants were to judge whether the probe item was one the items indicated by the second retrocue. Behavioural performance and two ERP components associated with either the efficiency of attentional selection (N2pc) or VWM maintenance (CDA/SPCN) were analysed. Both the N2pc and the CDA/SPCN are lateralized components which appear as enhanced negativity at posterior electrode sites contralateral to a respective visual hemifield.

The N2pc is usually observed about 200–300 ms after stimulus onset (e.g., [44,45]) and has been shown to be sensitive to the number of targets selected or individuated [46–50]. N2pc amplitude increased with an increasing number of targets, reaching an asymptote at three to four items. Importantly, N2pc asymptote has been shown to differ as a function of participants' behavioural efficiency [50] or tracking capacity [46]. Low performers exhibited weaker amplitude modulations with increasing target numbers, reaching an asymptote at a smaller number.

The CDA/SPCN appears approximately 275 ms after stimulus onset and typically persists throughout the retention interval, although the amplitude tends to decline over time, presumably due to an increase in ipsilateral activity [42]. The prevailing notion is that the CDA/SPCN reflects the number of items being maintained in VWM, as its amplitude is sensitive to the number of memory representations, reaches a limit when the mean capacity limit is exceeded, and reflects individual differences in VWM capacity [39]. There is, however, still some debate on what exactly it is the CDA/SPCN reflects. For example, CDA/SPCN amplitude appears to be sensitive to stimulus characteristics other than number, such as stimulus identity [51] or precision of representations [52]. It has also been used as an index of tracking load in multiple object tracking tasks, in which the CDA/SPCN was interpreted as an index of the number of attended items [46,53].

Behavioural performance and the CDA/SPCN were analysed to shed light on whether defocused items are still available for refocusing and recall. In our task, there was a relatively high likelihood (67%) that at least one initially uncued item would become relevant again, and different implications of this situation for intermittently defocused items were conceivable. First, if attentional selection in VWM was mainly employed to reduce memory load, these items might be excluded. Even with the refocusing likelihood of the present experiment, uncued items would remain irrelevant in a substantial number of trials, and excluding these items would relieve VWM by reducing memory load from four to two items. Behavioural performance for these items should then be close to chance level, and CDA/SPCN amplitudes in the cued conditions should be reduced after the first retrocue, as compared to the neutral retrocue condition. Second, in line with the protection account, intermittently defocused items might still be available for refocusing and recall. Overall, this should show in performance well above chance level, and a differential refocusing and weighting of items after the second retrocue is likely to reflect in diverging CDA/SPCN amplitudes in the cued conditions compared to after the first retrocue. A more detailed comparison of the continuously focused and intermittently defocused items in the two Add conditions will further elucidate the consequences of this refocusing: Upon refocusing, initially uncued items might either be "preserved"at their current strength, or they might be "boosted". Accordingly, performance for intermittently defocused items might be either worse than or equivalent to performance for continuously focused items. Moreover, the comparison of performance for the continuously focused items in the two Add conditions with performance for the continuously focused items in the Hold condition will provide insight into whether the inclusion of additional items in the FoA affects the maintenance of items already in the FoA.

To establish whether the individual efficiency of attentional deployment is related to the magnitude of the retrocueing benefit, correlations between the N2pc modulations following each retrocue and the behavioural retrocueing benefit were computed. Stronger N2pc modulations compared to the neutral condition, indicating higher attentional efficiency, were expected to be associated with larger retrocueing benefits.

Additionally, on the group level, analysis of the N2pc served to ensure that both retrocues induced differential attentional processing. As N2pc amplitude has been shown to scale with target number, N2pc amplitudes after the first retrocue were expected to be larger in the cued conditions than in the neutral condition, in which no attentional selection should take place. A further divergence of N2pc amplitudes in the cued conditions after the second compared to after the first retrocue was expected, with larger amplitudes in the Add conditions than in the Hold condition.

Methods

Ethics statement

The experiment was approved by the Ethics Committee of the Faculty of Psychology at Philipps-University Marburg, and conducted according to the principles of the Declaration of Helsinki. All participants provided informed written consent prior to the experiment.

Participants

Twenty-six students of Philipps-University Marburg participated in the experiment. Nine participants showed too many trials (> 40%) containing EEG artifacts. Analyses were performed on the remaining participants (11 female, 6 male, mean age = 22 years). All participants were naive to the purpose of the experiment, and had normal or corrected-to-normal visual acuity and normal colour vision. Visual acuity was tested with a Landolt C eye chart and colour vision with Ishihara's tests for colour deficiency [54].

Apparatus and stimuli

Participants were seated in a comfortable chair in a dimly lit and electrically shielded room, facing a monitor placed at a distance of approximately 104 cm from their eyes. They were instructed to maintain fixation during the experimental trials.

Stimuli were presented on a 22" screen (1680 x 1050 px) using E-Prime 2.0 software (Psychology Software Tools, Inc.). All stimuli were presented against a grey background. The colour of each memory item was randomly selected from a set of nine colours (blue, green, orange, pink, purple, red, turquoise, white and yellow). A given colour could appear no more than twice in an array, and only once in each hemifield. The colour of the test probe item was either randomly selected from the set of colours of the squares which were marked as relevant by the second retrocue (match trials) or from the set of colours not present in the attended hemifield on the respective trial (nonmatch trials). Each coloured square subtended 1.32° of visual angle in size. There were eight fixed positions for the eight squares of the memory array (four in each hemifield, two in each quadrant), which were arranged on an imaginary circle with a radius of approximately 4.95° of visual angle. Memory items within each hemifield were positioned at distances of 3.58° of visual angle from centre to centre. The memory items to the left and right of the vertical midline were positioned at a distance of 4.95° of visual angle from the centre of a square in one hemifield to the centre of the square on the other side of the vertical midline. The probe item was presented centrally to prevent any anticipatory external attentional orienting to other locations on the display. The precue subtended 1.10° of visual angle and the fixation dot 0.17° of visual angle. Retrocues were octagrams composed of two overlapping squares (1.10° of visual angle), with each corner pointing towards one of the locations of the memory items. For cueing specific items, the respective corners were blackened.

Procedure

The task is illustrated in Fig 1. A trial started with the presentation of an arrow presented just above the fixation dot for 200 ms, which pointed to one hemifield of the display. After an inter-stimulus interval of 800 ms, a memory array was presented for 200 ms, which consisted of four coloured squares in each hemifield. Participants had to memorize the squares in the previously indicated hemifield. After an interval of 800 ms, the first retrocue appeared for 200 ms. In the cued conditions, the first retrocue always marked either the upper or lower quadrant of the relevant hemifield. In the neutral condition the retrocue did not provide any spatial information as to the task-relevance of specific items. After another interval of 800 ms, the second retrocue was presented for 200 ms. In the cued conditions, the second retrocue was either identical to the first retrocue (Hold condition), additionally pointed to the adjacent square (Add1 condition), or marked the whole hemifield (Add2 condition). In the neutral condition, the second retrocue was identical to the first. Following the second retrocue and after an inter-stimulus interval of 800 ms, a test probe item was presented at the centre of the display until participants

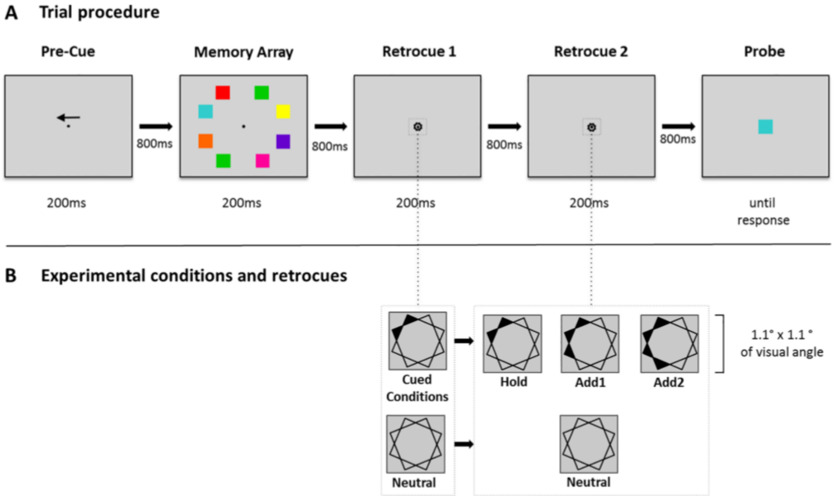

Fig 1. Trial procedure, experimental conditions and retrocues. A trial started with an arrow presented for 200 ms above fixation, indicating the relevant hemifield for that trial. After an inter-stimulus-interval of 800 ms, the memory array consisting of eight coloured squares was presented for 200 ms. Participants were instructed to memorize the squares in the respective hemifield. After a retention interval of 800 ms, a first retrocue was presented for 200 ms. In the cued conditions, this retrocue indicated two positions of previously presented memory items, i.e. the upper or lower quadrant of the respective hemifield. In the neutral condition, the retrocue provided no spatial information. After another interval of 800 ms, a second retrocue was presented for 200 ms. In the cued conditions, this retrocue was either identical to the first one (Hold), additionally pointed to the adjacent square (Add1), or marked the whole hemifield (Add2). In the neutral condition, the second retrocue was identical to the first one. After 800 ms, a central probe item was presented. Participants had to decide whether the probe was one of the items indicated by the second retrocue. Grey dotted squares show examples of the retrocues in the different experimental conditions.

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responded. Participants were to decide whether the probe item was the same as one of the items indicated by the second retrocue, responding match or nonmatch with a button press using their left or right index finger. The buttons were on the backside of a gamepad (Microsoft SideWinder USB) and the response assignment was balanced across participants. Accuracy was stressed, but in case of uncertainty participants were asked to decide spontaneously. The interval between trials varied randomly between 500 and 1000 ms.

There were 896 trials in total, randomized across 28 blocks of 32 trials each, with 224 trials per condition. This design introduced the following probability structure in the cued conditions. When the first retrocue was not neutral but marked two memory items, the likelihood that the second retrocue would additionally indicate at least one initially uncued item was 67%. Seeing as only the adjacent item was cued in the Add1 condition, the likelihood for that item to become relevant again was 67%, and the likelihood for the remaining fourth item only cued in the Add2 condition to become relevant again was 33%.

Testing took place on two consecutive days. The data of the first day's session were considered practice and not entered into the analyses. The EEG was recorded on the second day. Between blocks as well as in the middle of each block, participants were given the opportunity of a short rest. After the experiment, participants filled in a questionnaire to assess strategies and other factors that might affect performance.

Behavioural analyses

Trials with excessively long reaction times ($>$ 2.5 SD from mean RT calculated separately for each participant) were excluded from further analysis (Hold: 2.8%, Add1: 2.7%, Add2: 2.3%, Neutral: 3.6%; on average, 2.9% of all trials). Accuracy in percent and mean reaction time (only correct responses) were analysed.

EEG recording and analysis

The EEG was recorded continuously using BrainAmp amplifiers (Brain Products, Munich, Germany) from 64 Ag/AgCl electrodes (actiCAP) positioned according to the international modified 10–20 system. Vertical (vEOG) and horizontal electrooculogram (hEOG) were recorded as the voltage difference between electrodes positioned above and below, and to the left and right of the eyes, respectively. All channels were referenced to FCz and re-referenced offline to the average of all electrodes. Electrode impedances were kept below 5 kΩ. The sampling rate was 1000 Hz with a high cutoff filter of 250 Hz (half-amplitude cutoff, 30dB/oct) and a low cutoff filter of 0.016 Hz (half-amplitude cutoff, 6dB/oct).

The EEG was segmented into epochs of 3200 ms, starting 200 ms prior to the onset of the memory array and ending at the onset of the test probe display. The time period from -200 ms to 0 was used for baseline correction. Trials with response errors were excluded from analysis. Trials with blinks (vEOG $>$ 80 μv; on average, 6% of all trials) and eye movements (hEOG $>$ 50 μv; on average, 10% of all trials) were excluded from all channels. Additionally, trials in channels with other artefacts were excluded if the amplitude exceeded ± 80 μv. To assess residual eye movements towards the cued hemifield, the hEOG was quantified for each cued hemifield, condition and time window of analysis. The maximum deflection was 4.02 μv, which can be considered equivalent to an eye movement of about 0.25° [55]. In order to isolate the N2pc and the CDA/SPCN components, left (PO3, PO7) and right (PO4, PO8) parieto-occipital electrodes were averaged for each visual hemifield and experimental condition. Difference waves were then calculated by subtracting activity ipsilateral from activity contralateral to the respective hemifield.

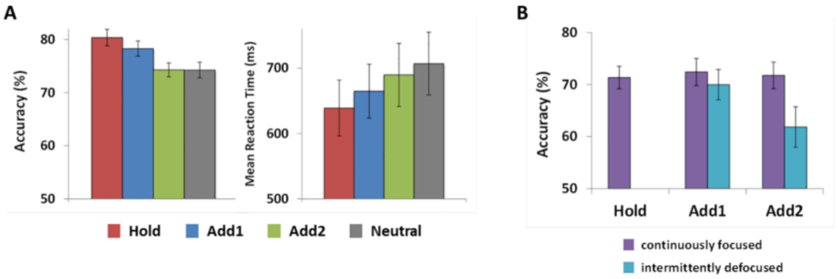

Fig 2. Behavioural results. A The left panel shows accuracy in percent and the right panel mean reaction time in ms for each experimental condition (Hold in red, Add1 in blue, Add2 in green and Neutral in grey). **B** Accuracy in percent for the different types of match probes in the Add conditions and in the Hold condition (continuously focused match probes in violet, intermittently defocused match probes in turquoise). Error bars show the standard errors of the means.

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Results

Behavioural results

Behavioural results are plotted in Fig 2. Separate one-way ANOVAs were computed for accuracy and reaction time. Performance differed across conditions, with respect to both accuracy [$F_{(3,48)} = 14.95$, $p < .001$, partial $\eta^2 = .48$] and reaction time [$F_{(3,48)} = 19.07$, $p < .001$, partial $\eta^2 = .54$]: Participants performed best in the Hold condition [*accuracy* 80.38 ± 1.6; *RT* 639.01 ± 42.74], followed by Add1 [*accuracy* 78.31 ± 1.4; *RT* 664.86 ± 41.17], Add2 [*accuracy* 74.29 ± 1.3; *RT* 689.74 ± 48.25], and the neutral condition [*accuracy* 74.28 ± 1.5; *RT* 706.98 ± 48.02] (see Fig 2A). ANOVA contrasts revealed significant differences between Hold and Neutral [*accuracy* $F_{(1,16)} = 23.59$, $p < .001$, partial $\eta^2 = .60$; *RT* $F_{(1,16)} = 65.55$, $p < .001$, partial $\eta^2 = .80$] and Add1 and Neutral [*accuracy* $F_{(1,16)} = 14.28$, $p = .002$, partial $\eta^2 = .47$; *RT* $F_{(1,16)} = 18.01$, $p = .001$, partial $\eta^2 = .53$], and for reaction time also between Add2 and Neutral [$F_{(1,16)} = 5.08$, $p = .039$, partial $\eta^2 = .24$].

To rule out that the effects were driven by an external shift of attention induced by the retrocues, a behavioural control experiment was conducted. In this control experiment, the retrocues had no lateralized components. The results replicated the benefits observed in the present experiment: Performance was best in the Hold condition (81.18 ± 1.9), followed by Add1 (78.97 ± 1.6), the Add2 (75.13 ± 1.2) and the neutral condition (74.61 ± 1.8) (see S4 Fig for the experimental conditions, retrocues and results of this control experiment). These findings indicate that the retrocueing benefits observed in the present experiment were not driven by the lateralized aspects of the retrocues, but were the result of the voluntary focusing of attention onto representations maintained in VWM.

In a second step, results in the Add1 and Add2 condition were further analysed in order to separate accuracy performance for continuously focused and intermittently defocused match probe items (see Fig 2B). First, a two-way ANOVA with the factors condition (Add1 vs. Add2) and probe item type (continuously focused vs. intermittently defocused) was computed. Second, t-tests served to compare the intermittently defocused match probe items in each Add condition against the chance level of 50%. Third, t-tests comparing the continuously focused match probes in each Add condition against the match probes in the Hold condition were computed. This was done to test whether performance for continuously focused items in the Add conditions was equivalent to performance for the continuously focused items in the Hold condition, even though the Add condition required the additional focusing of one or two more items. The ANOVA revealed a main effect of probe item type [$F_{(1,16)} = 5.96$, $p = .027$, partial $\eta^2 = .27$] with lower accuracy for intermittently defocused items, and an interaction between the factors of condition and probe type [$F_{(1,16)} = 4.93$, $p = .048$, partial $\eta^2 = .22$], attributable to a larger difference between accuracy for continuously focused and intermittently defocused items in the Add2 condition compared to the Add1 condition. Even though accuracy for intermittently defocused items was lower than accuracy for continuously focused items, it was well above chance level in both the Add1 [$t_{(16)} = 6.85$, $p < .001$] and the Add2 condition [$t_{(16)} = 3.04$, $p = .008$]. Performance for the continuously focused items in the Add1 [$t_{(16)} = 0.54$, $p = .595$] and in the Add2 condition [$t_{(16)} = 0.32$, $p = .76$] was equivalent to performance for the match probes in the Hold condition.

Electrophysiological results

ERP results are plotted in Fig 3. For N2pc analyses, mean amplitudes were computed for time intervals from 200 to 300 ms after the onset of each retrocue. For CDA/SPCN analyses, mean amplitudes were computed for three time intervals, namely from 450 to 650 ms after the onset of the memory array and after each retrocue. This time window was chosen based on the interval following the memory array, for which a CDA/SPCN but no differential effects between conditions were expected. To determine the presence of the lateralized components N2pc and CDA/SPCN, two-way ANOVAs were run on the mean amplitudes for these time windows, with the factors condition (Hold, Add1, Add2, and Neutral) and laterality (ipsilateral and contralateral). For the interval following the first retrocue, an additional t-test was computed to compare the cued conditions (Hold, Add1, and Add2) directly against the neutral condition. For the cued conditions, additional three-way repeated measures ANOVAs with the factors of retrocue (first and second), condition (Hold, Add1, and Add2) and laterality (ipsilateral and contralateral) were run for both N2pc and CDA/SPCN time windows of analysis.

An N2pc was present both after the first [$F_{(1,16)} = 20.75$, $p < .001$, partial $\eta^2 = .57$,] and second retrocue [$F_{(1,16)} = 24.10$, $p < .001$, partial $\eta^2 = .60$]. Interactions between condition and laterality after both the first [$F_{(3,48)} = 7.41$, $p = .002$, partial $\eta^2 = .23$, $\varepsilon = .62$] and the second

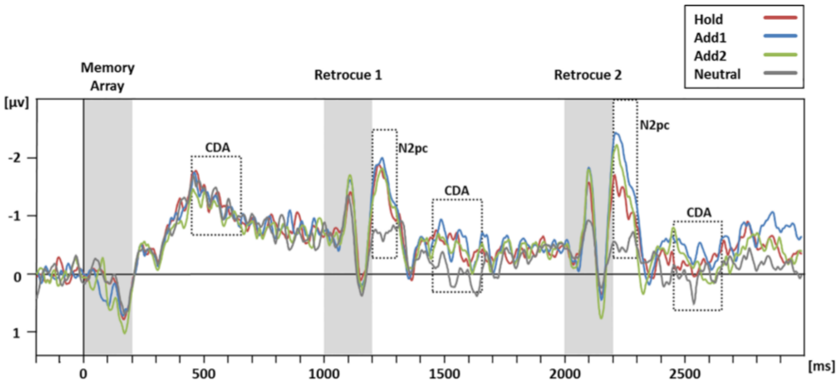

Fig 3. Grand-averaged ERP difference waves (contralateral activity minus ipsilateral activity). Difference waves are shown for the experimental conditions (Hold in red, Add1 in blue, Add2 in green and Neutral in grey) time-locked to the onset of the memory array averaged across parieto-occipital electrodes (PO3/PO4, PO7/PO8). Time windows of stimulus presentations are shaded in grey, the time windows for N2pc and CDA/SPCN analyses are indicated by grey dotted squares. For illustration purposes the waveforms were lowpass filtered (half-amplitude cutoff at 35 Hz, 24 dB/oct).

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retrocue [$F_{(3,48)} = 11.15$, $p < .001$, partial $\eta^2 = .41$, $\varepsilon = .78$] revealed differences in lateralized activity and the following more specific analyses provided more insight into these differences between conditions: After the first retrocue, the N2pc observed in the cued conditions was larger than the N2pc in the neutral condition [$t_{(16)} = 3.29$, $p = .005$]. Following the second retrocue, mean N2pc amplitudes in the cued conditions diverged compared to the time window following the first retrocue. This was revealed by a three-way interaction of the factors retrocue, condition and laterality [$F_{(2,32)} = 4.32$, $p = .022$, partial $\eta^2 = .21$]. N2pc amplitudes after the second retrocue were larger in the Add1 than in the Hold condition [$t_{(16)} = 3.77$, $p = .001$]. N2pc amplitudes in the Add2 and the Hold conditions [$t_{(16)} = 1.58$, $p = .067$], and in the Add1 and Add2 conditions [$t_{(16)} = 1.51$, $p = .075$] did not differ significantly.

After presentation of the memory array, a CDA/SPCN was observed [$F_{(1,16)} = 87.98$, $p < .001$, partial $\eta^2 = .85$], which was equivalent in size for all conditions [$F_{(3,48)} = 0.64$, $p = .590$, partial $\eta^2 = .04$]. There was a significant overall CDA/SPCN [$F_{(1,16)} = 7.46$, $p = .015$, partial $\eta^2 = .32$] and an interaction between condition and laterality [$F_{(3,48)} = 4.12$, $p = .011$, partial $\eta^2 = .21$] only after the first retrocue. Similar to the N2pc results, the CDA/SPCN after the first retrocue was larger in the cued conditions than in the neutral condition [$t_{(16)} = 3.12$, $p = .007$]. There was no divergence of CDA/SPCN amplitudes in the cued conditions after the second retrocue compared to the time window following the first retrocue.

To ensure that the observed patterns in N2pc and CDA/SPCN modulations were not driven by effects in early sensory potentials attributable to different processing of the cues, all analyses for the time windows after each retrocue were rerun with the retrocue presentation time as baseline (i.e., 1000 ms to 1200 ms for the first retrocue, and 2000 ms to 2200 ms for the second retrocue). The observed patterns and all reported effects remained.

Scalp distributions of N2pc and CDA/SPCN were compared for the time window following the first retrocue. This interval was chosen because ERPs could be collapsed across the cued conditions, leading to more reliable measures. Difference waves for parietal, parieto-occipital and occipital electrode pairs were calculated, and the respective activity was normalized following the procedure described by [56]. A two-way ANOVA with the factors of time window (1200–1300, 1450–1650) and electrode position (seven posterior electrode pairs) revealed an interaction [$F_{(6,96)} = 6.16$, $p < .001$, partial $\eta^2 = .28$, $\varepsilon = .56$], demonstrating distinct scalp distributions. The N2pc showed a more ventral, and the CDA/SPCN a more dorsal distribution (see S3 Fig), which is in line with previous findings [42,46].

Correlations between behavioural and electrophysiological measures

Scatter plots are shown in Fig 4. One-tailed correlations (Pearson's correlation coefficient, *r*) were computed between individual N2pc amplitudes and accuracy, and between CDA/SPCN amplitudes and accuracy. This was done for the Add1 condition relative to baseline by subtracting each participant's value in the neutral condition from the respective value in the Add1 condition. The Add1 condition was chosen, because it required attentional selection after each retrocue (unlike the Hold condition) and included a number of items that is well within mean VWM capacity (unlike the Add2 condition). Split-half reliabilities (Pearson's correlation coefficient, *r*; one-tailed) were computed from even-numbered and odd-numbered trials and corrected for the full number of trials using the Spearman-Brown formula [57,58] (reported are corrected correlation coefficients and the uncorrected p-values). These were significant for accuracy ($r = .73$, $p = .007$), for the N2pc after both the first ($r = .67$, $p = .020$) and the second retrocue ($r = .71$, $p = .010$), and for the CDA/SPCN after the second ($r = .74$, $p = .006$), but not after the first retrocue ($r = .32$, $p = .232$).

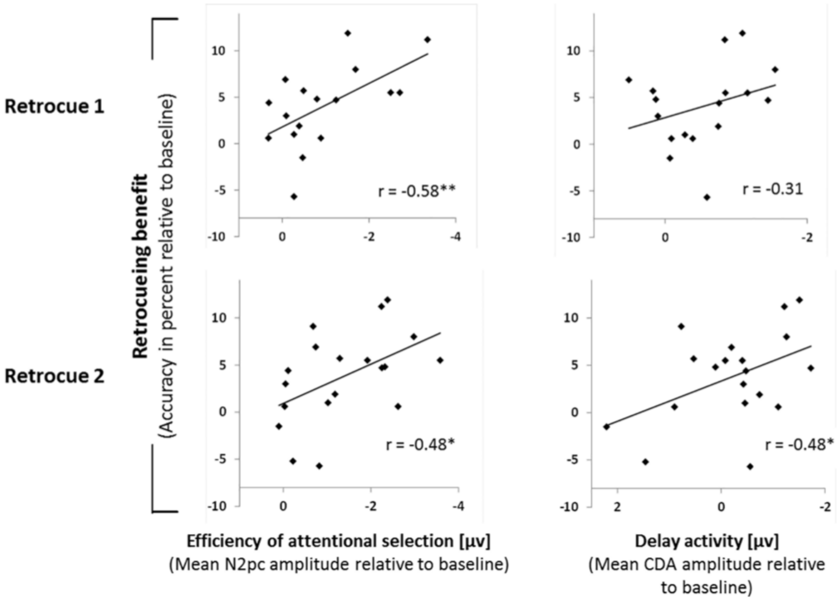

Fig 4. Correlations between behavioural and ERP results. The first column shows correlations between N2pc amplitude and accuracy results, and the second column correlations between CDA/SPCN amplitudes and accuracy results. For correlations in the top row, ERP measures were calculated from the time windows following the first retrocue, for correlations in the bottom row, ERP measures were calculated from the time windows following the second retrocue. All measures were computed for the Add1 condition and relative to baseline, i.e. the value of each measure in the neutral condition was subtracted from the value of the respective measure in the Add1 condition.

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Significant correlations were found between the retrocueing benefit and N2pc amplitude after both the first (r = -.576, p = .008) and the second retrocue (r = -.477, p = .027) (Fig 4, first column). The correlation between CDA/SPCN amplitude and retrocueing benefit was significant for the time window following the second retrocue (r = -.483, p = .025), but not for the time window following the first retrocue (r = -.307, p = .115) (Fig 4, second column). According to these correlations, the larger the individual efficiency of attentional selection (as indicated by N2pc differences) and the stronger the maintenance-associated activity, the larger the individual retrocueing benefit.

Discussion

With the present experiment, we addressed two questions. First, we asked whether defocused items remain available in a scenario in which these items may become task-relevant again. The results showed that this was the case: defocused items could later be refocused and successfully recalled. Thus, the defocusing of items does not necessarily lead to their loss. Performance for these intermittently defocused items was, however, worse than for continuously focused items, indicating that a cost is associated with defocusing, and that refocusing an item cannot boost it back to the initial level. This cost appeared to be higher when the likelihood to become task-relevant was lower: Performance for intermittently defocused items was worse in the Add2 condition than in the Add1 condition ($t_{(16)} = 2.85$, p = .006; see Fig 2B). Whereas the likelihood to become task-relevant again was 67% for the intermittently defocused item in the Add1 condition (this item was always adjacent to the items cued by the first retrocue, and would be required to be refocused in both the Add1 and Add2 conditions), it was only 50%, on average, for the intermittently defocused items in the Add2 condition (67% for the item adjacent to the items cued by the first retrocue, and 33% for the nonadjacent item).

Similar conclusions as to the importance of task context and retrocue reliability in determining the fate of defocused items have been reached by recent studies. Zokaei et al. [59] found that an item that remains behaviourally relevant can be maintained outside the FoA and refocused, but that an item rendered very unlikely to be probed is lost from VWM. Similarly, Gunseli et al. [60] observed costs of invalid retrocueing only when the retrocue had a high reliability (80%), but not when it had a low reliability (50%). Thus, irrelevant items can be removed, or maintained items can be strategically weighted with respect to their relevance and according to a given probability structure. In the same vein, van Moorselaar et al. [61] suggested that representations in VWM can adopt different states depending on their deemed relevance, and that these states can be flexibly adjusted to changing task demands. Accordingly, items can be maintained inside as well as outside the FoA, with different degrees of robustness or vulnerability, respectively. Taken together with findings demonstrating that it is principally possible to exclude representations from memory following an almost always valid cue presented during the maintenance interval [43], the present results add support to the notion of a high flexibility of visual working memory when it comes to making the most out of its limited resources given a specific situation.

Importantly, the inclusion of intermittently defocused items in the FoA in the two Add conditions did not affect maintenance of the continuously focused items. Focused representations seem to be protected from degradation, and this protection appears to be unaffected by an expansion of the FoA and the inclusion of additional representations. Thus, the particularly robust maintenance inside the FoA provides a reliable means to ensure that the most relevant information is prioritized and kept available.

Given the likelihood that initially uncued items would become relevant again upon presentation of the second retrocue, one may question whether participants did, in fact, defocus these items. Based on overall performance (Fig 2A), one may argue that participants held on to all items after the first retrocue, and only dropped the items not cued by the second retrocue. Overall performance would then reflect memory load at the time of retrieval. However, this hypothesis cannot account for the differences in performance for continuously cued ("focused") and intermittently uncued ("defocused") items in the Add conditions: Performance for these items should be equal if the first retrocue was ignored, and they should be equally affected by differences in memory load. Instead, performance for continuously cued items was at the same level in all cued conditions, and performance for intermittently uncued items reflected the likelihood with which these items might become relevant again. These findings clearly demonstrate that the information maintained in VWM was weighted according to the probability structure introduced by the cues. How exactly this behaviourally evident sensitivity to a given probability structure is implemented at the representational level in VWM cannot be conclusively determined based on our own findings. In light of evidence for different representational states in VWM that are linked to the attentional status of representations [24–28], we argue that this weighting is implemented by maintenance within and outside the FoA, and that, consequently, initially uncued items were indeed defocused. (Another explanation for the sensitivity to the probability structure could be based on a different interpretation of mean performance. According to this interpretation, mean performance would not be representative of what happened in each trial (i.e., defocusing), but would be a mixture of different processes in different trials (i.e., continued maintenance vs. removal).)

No converging conclusions with regard to this first question we addressed could be drawn from the CDA/SPCN results. Implications of the present findings for the interpretation of the CDA/SPCN shall be discussed in more detail below.

Second, we asked whether the individual efficiency of attentional orienting within VWM was related to the magnitude of the retrocueing benefit. Indeed, stronger N2pc modulations indicating a higher attentional efficiency were associated with larger retrocueing benefits. The finding that individual differences in attentional selection, as indicated by the N2pc, were related to the updating of VWM following retrocues adds to a growing body of literature investigating individual differences in attentional control related to working memory functions. For example, Vogel et al. [62] found differences in the individual efficiency with which only relevant items were selected for encoding, and Fukuda and Vogel [63,64] found that individuals with a high working memory capacity were better at resisting attentional capture by irrelevant distractors. However, as discussed below, the cognitive processes reflected by the N2pc in the present experiment are disputable. Consequently, the relationship between individual N2pc modulations and retrocueing benefits might not be as straightforward as suggested by these findings.

The CDA/SPCN and the internal focus of attention

The prevailing view of the CDA/SPCN is that it reflects the number of items maintained in VWM. This notion, however, cannot account for the present findings: CDA/SPCN amplitudes did not mirror memory load in the experimental conditions. This was most obvious after the first retrocue, when memory load in the neutral condition was at least as high as in the cued conditions, but CDA/SPCN amplitude was smaller. After the second retrocue, no differences between experimental conditions and, in fact, no overall CDA/SPCN was observed. This may be related to the long trial duration, as the CDA/SPCN has been shown to “naturally” decline over time [42].

The finding of larger amplitudes in the cued conditions than in the neutral condition after the first retrocue could be seen as at variance with those of Kuo et al. [11]. In particular, they observed a stronger CDA/SPCN attenuation after informative retrocues than after neutral retrocues. There is one important difference between our task and the one used by Kuo et al. [11], which could account for the divergent findings. Whereas in their experiments, uncued items were never tested, in our experiment, there was a relatively high likelihood that the initially uncued items would become relevant again. As discussed above, this likelihood might be a crucial factor in determining what happens with uncued information. Thus, the retrocue might have resulted in the removal of uncued information in the experiments by Kuo et al. [11], whereas in our experiment, it might have induced an updating process to differentially weigh and maintain all items. It seems reasonable to assume that such different implications of the cues would yield different patterns of CDA/SPCN amplitudes.

Our findings suggest that the CDA/SPCN is, at least to some degree, associated with the internal FoA. Note that we do not suggest a reinterpretation of the CDA/SPCN as an index of the amount of items in the FoA, but only that there is a link to attentional processes involved in updating VWM according to changes in the task-relevance of specific items, that is, in adjusting the FoA. This idea would account for the pattern of CDA/SPCN amplitudes observed after the memory array and after the first retrocue. After the memory array, the initial FoA was identical in all conditions, which was reflected in equivalent CDA/SPCN amplitudes. After the first retrocue, differential weighting of maintained items was induced in the cued conditions, yielding larger CDA/SPCN amplitudes in the cued compared to the neutral condition.

The conclusions suggested by our present findings are consistent with some previous studies linking the CDA/SPCN to attentional processes. Evidence is provided by neuroimaging studies. The most discussed candidate for the neural source of the CDA/SPCN is the intra-parietal sulcus (IPS). Several studies have observed load-dependent (BOLD) activations reaching a plateau at the mean VWM capacity limit on the group level, which was correlated with VWM capacity on the individual level [65–68]. Load-dependent activations in the IPS have also been observed in tracking tasks varying the attentional load [69,70]. This matches findings on the CDA/SPCN that typically exhibits tracking load-dependent amplitudes [46,53]. Further evidence comes from studies not directly investigating the CDA/SPCN, but the nature of delay activity per se. Two studies using MVPA recorded in event-related fMRI [26] and of electrophysiological activity [24] found evidence for delay activity only for items maintained in the FoA. The authors call into question the long-standing idea that active maintenance is necessary for short-term retention. One does, however, not need to go this far to presume that the CDA/SPCN is related to the internal FoA, given that in most studies establishing the link between CDA/SPCN amplitude and maintained items, the attending and memorizing of items was confounded (e.g., [42,62,71]).

The N2pc—an electrophysiological marker of selection in VWM?

An N2pc was observed following each retrocue, exhibiting an amplitude modulation that reflected the attentional demands posed by the respective retrocue and that, on the individual level, was related to the magnitude of the benefit for focused items. After the first retrocue, N2pc amplitude was larger in the cued conditions as compared to the neutral condition, in which no attentional updating of VWM was required. After the second retrocue, N2pc amplitudes diverged in the cued conditions compared to after the first retrocue, with larger amplitudes in the Add conditions, in which further updating was necessary. While the N2pc as an index of attention deployment towards targets in extrapersonal space has been extensively studied, only few studies employed this ERP to shed light on mnemonic processes. An N2pc response has been found in studies comparing visual search to search in VWM, with the target being presented before or after a search array [15,72]. While the N2pc for VWM search was temporally and largely topographically equivalent to the N2pc for visual search, it was insensitive to search load. In these tasks, however, only one target had to be selected and the number of distractors, that is, of memory load in VWM search, was varied. In the present study, in contrast, initial memory load was constant and the number of selected memory items was varied. Similar in this respect are multiple object tracking studies asking participants to memorize and track different numbers of objects. Drew and Vogel [46] recorded ERPs during a tracking task, and observed an N2pc that was strongly modulated by the number of target items. This fits nicely to the observation made in the present study, that the larger the number of items to be selected, the larger N2pc amplitude. Importantly, moreover, Drew and Vogel [46] demonstrated that N2pc amplitude reached an asymptote when the mean capacity limit of three to four items [7,8] was exceeded. They also observed that for low-capacity performers, amplitude dropped below the three-item level for set sizes beyond the capacity limit. A similar pattern emerged in the present experiment: N2pc amplitude was larger the more items were to be selected, with the exception of the Add2 condition, which required participants to attend to four items. Here, N2pc amplitude slightly dropped below the level of the Add1 condition (Fig 3). It appears that asking participants to attend to a number of items exceeding their VWM capacity has a disruptive effect on the mechanisms selecting targets in memory, and thus on updating items in VWM according to changed task relevance.

Even though the N2pc responses are consistent with what one would expect for the selection of VWM representations in the present paradigm and fit with previous findings discussed above, it is possible that the N2pc observed in the present study reflected the focusing of attention onto the cue itself. This would have resulted in the same pattern of results. Van Velzen and Eimer [73] showed that centrally presented cues with lateralized components can elicit lateralized ERPs, and concluded that under such conditions, the N2pc reflects the selection of relevant aspects of the cue. Although it should be noted that the cues employed by Van Velzen and Eimer [73] were larger (3.5° vs. 1.1° in the present experiment) and thus extended farther into the visual hemifields, it is possible that this is what was being observed in the present study. According to this alternative scenario, the N2pc responses following the retrocues reflected the selection of the individual corners of the cues, yielding larger N2pc amplitudes in the cued conditions than in the neutral condition after the first retrocue, and even larger amplitudes in the Add conditions than in the Hold condition after the second retrocue. The correlations would correspondingly indicate that individuals who were better at selecting and individuating the corners of the cue were the ones with larger retrocueing benefits. This correlation would presumably still be mediated by better attentional selection in VWM that relies on better attentional processing of the cue. Thus, the N2pc observed here might, in fact, not be a direct electrophysiological correlate of the internal selection of information maintained in VWM, but a correlate of the external selection of the cue, which is a prerequisite for this internal selection. Given that we cannot entirely rule out this alternative scenario, any conclusions drawn on the present N2pc results should be taken with caution.

Conclusions

The present experiment provides support for the assumption that within VWM, attentional selection is employed to protect those representations which hold particular relevance for our current goals. Defocused representations that may become relevant again are not lost, but can be refocused and recalled. However, defocusing comes at a cost, and memory for the corresponding items is worse than for items that are continuously focused and protected. These findings indicate that maintained information in VWM can be flexibly weighted according to its relevance. The results also provide new insight into the cognitive processes reflected by the CDA/SPCN: Taken together with other findings discussed above, they suggest a linkage between the CDA/SPCN and attentional processes.

Supporting Information

S1 Data. Accuracy.
(XLS)

S2 Data. Reaction Time.
(XLS)

S3 Data. Control Experiment (Accuracy).
(XLS)

S4 Data. Electrophysiological data. Mean amplitudes of ipsilateral and contralateral activity (Sheet 1) and of the difference waves (Sheet 2) for all CDA/SPCN and N2pc time windows of analysis.
(XLS)

S5 Data. Correlation data. Accuracy and N2pc and CDA/SPCN amplitudes for the windows of analysis after the retrocues in the Add1 condition relative to baseline (i.e., minus the values

in the neutral condition), as well as all of these measures computed separately from even-numbered and odd-numbered trials.
(XLS)

S6 Data. Scalp distribution data (normalized).
(XLS)

S1 Fig. Grand-averaged ERPs. ERPs are shown for the experimental conditions (Hold in red, Add1 in blue, Add2 in green and Neutral in grey) time-locked to the onset of the memory array averaged across parieto-occipital electrodes (PO3/PO4, PO7/PO8). Time windows of stimulus presentations are shaded in grey. For illustration purposes, the waveforms were low-pass filtered (half- amplitude cutoff at 35 Hz, 24 dB/oct).
(TIF)

S2 Fig. Grand-averaged contralateral and ipsilateral activity. Contralateral (dashed lines) and ipsilateral (solid lines) activity is shown separately for the four conditions, time-locked to the onset of the memory array and averaged across parieto-occipital electrodes (PO3/PO4, PO7/PO8). Time windows of stimulus presentations are shaded in grey. For illustration purposes, the waveforms were lowpass filtered (half-amplitude cutoff at 35 Hz, 24 dB/oct).
(TIF)

S3 Fig. Scalp distribution maps. Scalp distributions of the N2pc and the CDA/SPCN for the time windows of analysis following the first retrocue: 1200–1300 ms for the N2pc and 1450–1650 ms for the CDA/SPCN, time-locked to the onset of the memory array. The left panel shows the scalp distribution of the N2pc on a scale from -2.0 μv to 0 μv, the right panel shows the scalp distribution of the CDA/SPCN on a scale from -0.5 μv to 0 μv. Each panel shows the difference between contralateral and ipsilateral activity averaged across the cued conditions (Hold, Add1 and Add2) and across hemispheres.
(TIF)

S4 Fig. Experimental conditions, retrocues and results of the control experiment. A In the cued conditions, the first retrocue indicated two positions of previously presented memory items, i.e. the upper or lower quadrant of the respective hemifield. In the neutral condition, the retrocue provided no spatial information. The second retrocue was in the cued conditions either identical to the first one (Hold), additionally marked the adjacent position (Add1) or the whole hemifield (Add2). In the neutral condition, the second retrocue was identical to the first one. **B** Accuracy in percent for each experimental condition (Hold in red, Add1 in blue, Add2 in green, Switch in orange and Neutral in grey). Error bars show the standard errors of the means.
(TIF)

Author Contributions

Conceived and designed the experiments: AH AS. Performed the experiments: AH. Analyzed the data: AH. Wrote the paper: AH AS.

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Study II

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Feature-based and spatial attentional selection in visual working memory

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Abstract The contents of visual working memory (VWM) can be modulated by spatial cues presented during the maintenance interval ("retrocues"). Here, we examined whether attentional selection of representations in VWM can also be based on features. In addition, we investigated whether the mechanisms of feature-based and spatial attention in VWM differ with respect to parallel access to noncontiguous locations. In two experiments, we tested the efficacy of valid retrocues relying on different kinds of information. Specifically, participants were presented with a typical spatial retrocue pointing to two locations, a symbolic spatial retrocue (numbers mapping onto two locations), and two feature-based retrocues: a color retrocue (a blob of the same color as two of the items) and a shape retrocue (an outline of the shape of two of the items). The two cued items were presented at either contiguous or noncontiguous locations. Overall retrocueing benefits, as compared to a neutral condition, were observed for all retrocue types. Whereas feature-based retrocues yielded benefits for cued items presented at both contiguous and noncontiguous locations, spatial retrocues were only effective when the cued items had been presented at contiguous locations. These findings demonstrate that attentional selection and updating in VWM can operate on different kinds of information, allowing for a flexible and efficient use of this limited system. The observation that the representations of items presented at noncontiguous locations could only be reliably selected with feature-based retrocues suggests that feature-based and spatial attentional selection in VWM rely on different mechanisms, as has been shown for attentional orienting in the external world.

Keywords Working memory · Attention · Short-term memory

Introduction

Maintaining and manipulating visual information is a core capability that is essential not only for higher cognitive functions, but also for simple tasks that we perform hundreds of times every day. Given the highly limited capacity of visual working memory (VWM; Cowan, 2001; Luck & Vogel, 1997), there is a need to update its contents in a dynamic manner. In recent years, it has been shown that attention can be oriented toward representations in visual working memory (VWM), yielding better memory for the respective items in the focus of attention (e.g., Astle, Summerfield, Griffin, & Nobre, 2012; Griffin & Nobre, 2003; Murray, Nobre, Clark, Cravo, & Stokes, 2013). This allows for a flexible modulation of VWM contents: Depending on how relevant information is or how likely it is to become relevant again, information can be maintained within or outside the focus of attention, or it can even be irretrievably excluded from memory (Heuer & Schubö 2016, manuscript submitted for publication; Williams, Hong, Kang, Carlisle, & Woodman, 2013; Zokaei, Ning, Manohar, Feredoes, & Husain, 2014). Experimentally, attentional selection in VWM is typically investigated with so-called *retrocues*, which are presented during the retention interval of a VWM task and mark specific items as more behaviorally relevant than others by cueing the locations at which these had been presented.

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It has proven fruitful to study the deployment of attention in the mnemonic domain in relation to the already better understood deployment of attention in the perceptual domain. Attentional orienting in these two domains will in the following sections be referred to as *internal* and *external* attention (Chun, Golomb, & Turk-Browne, 2011; Kiyonaga & Egner, 2013). Previous research has shown that internal and external attention recruit a largely overlapping neural network involving parietal, frontal, and occipital areas (Nee & Jonides, 2009; Nobre et al., 2004; Tamber-Rosenau, Esterman, Chiu, & Yantis, 2011), and that they are strikingly similar with respect to the benefits and costs resulting from valid and invalid cueing (Astle, Scerif, Kuo, & Nobre, 2009; Griffin & Nobre, 2003). Building on this demonstration of a high degree of correspondence, in the present experiments we investigated whether internal attention is also similar to external attention with regard to the type of information that can be used to guide attention.

Feature-based and spatial attentional orienting

For external attention, the types of stimulus characteristics that can be used for attentional selection have been studied extensively. For example, spatial locations (Carrasco, 2011; Posner, 1980); single features such as the color, shape, or direction of motion (e.g., Bichot, Rossi, & Desimone, 2005; Martinez-Trujillo & Treue, 2004; Saenz, Buraĉas, & Boynton, 2002); a conjunction of features (e.g., Buracas & Albright, 2009; Nordfang & Wolfe, 2014; Weidner & Müller, 2013); or categories of more complex objects, such as faces (e.g., New, Cosmides, & Tooby, 2007; Serences, Schwarzbach, Courtney, Golay, & Yantis, 2004; Theeuwes & Van der Stigchel, 2006) can all be attentionally selected. At a broader level, a distinction is typically drawn between feature-based and spatial attention (e.g., Carrasco, 2011; Eimer, 2014).

Attentional mechanisms operating on different types of information are important for optimizing the visual system, because they allow us to flexibly rely on whatever kind of relevant information is available. When we are meeting a friend in a crowded place, we may monitor the area surrounding the fountain where he said he would wait (spatial attention) and look out for blue objects, because we expect him to wear a blue jacket (feature-based attention). Or we may have no idea where we left that scarf, so we will scan the room for yellow objects.

In light of the limited capacity of VWM, a similar flexibility with respect to the type of maintained information that can be attentionally selected would be highly advantageous. Typically, however, the investigation of internal attention has employed retrocues that provide spatial information as to the behavioral relevance of objects previously presented at specific locations. In fact, studies have almost exclusively been based on spatial retrocues (e.g., Astle et al., 2012; Matsukura, Luck, & Vecera, 2007; Nobre et al., 2004; Sligte, Scholte, & Lamme, 2008) or ones that cued entire object categories (Lepsien & Nobre, 2007; Lepsien, Thornton, & Nobre, 2011). Only a few studies have used retrocues relying on other types of information, and the question of whether the distinction between feature-based and spatial attention also applies to internal attention has so far been largely neglected.

The first to systematically investigate different retrocue types were Berryhill, Richmond, Shay, and Olson (2012). They presented participants with a retrocue consisting of either a number that mapped onto the location of one item, a dash appearing at the location of one item, or an arrow pointing to one location. A retrocueing benefit, as compared to a condition with an uninformative neutral cue, was only found for arrow retrocues, from which the authors concluded that this cueing benefit does not generalize across various cue types, as has been demonstrated for the perceptual domain. These null effects for other types of retrocues, however, might have been due to experimental details that left participants unable or unwilling to make use of the cue. For example, the interval between the retrocue and the probe item was unusually short (400 ms), and especially a symbolic retrocue such as a number might require more time to be processed. Moreover, the retrocue types varied randomly on a trial-by-trial basis, and such a frequent switch between retrocue types might require additional effort. Thus, although the findings of Berryhill et al. demonstrated that the arrow retrocue is particularly robust, they do not necessarily preclude that other retrocue types could also yield a benefit for cued items. Indeed, Pertzov, Bays, Joseph, and Husain (2013) found that retrocueing an object's color was just as advantageous as retrocueing an object's spatial location, in a task in which memory for a third feature (orientation) was assessed. Similarly, Li and Saiki (2014) observed equivalent benefits for color and location retrocues when color–location conjunctions were to be memorized. However, as was pointed out by Pertzov et al., it is possible that participants still adopted a spatial strategy when presented with a feature-based retrocue. They might have used the information provided by the cue, such as the color of the item, to retrieve information about the item's location and then to deploy their attention to that location. If this were the case, feature-based and spatial retrocues would rely on the same space-based mechanism of attention. To examine whether these two types of retrocues rely on the same or on different attentional mechanisms, one can draw on certain differences between feature-based and spatial attention that have been established for the external domain.

Allocating attention to noncontiguous locations

For external attention, there is evidence that feature-based and spatial attention operate differently and rely on slightly different cortical regions (Giesbrecht, Woldorff, Song, & Mangun, 2003;

Greenberg, Esterman, Wilson, Serences, & Yantis, 2010; Schenkluhn, Ruff, Heinen, & Chambers, 2008; Slagter et al., 2007; Vandenberghe, Gitelman, Parrish, & Mesulam, 2001). Of particular interest in the present context are differences between feature-based and spatial mechanisms in the allocation of attention to noncontiguous locations. Feature-based attention has been shown to modulate the activity of neurons throughout visual cortex, enhancing the processing of stimuli with behaviorally relevant features across the entire visual field, within and outside the spatial locus of attention (Maunsell & Treue, 2006; Saenz et al., 2002; Sàenz, Buracâs, & Boynton, 2003; Treue, 2003). Thus, feature-based attention can be allocated in parallel to multiple locations. Whether the same holds true for spatial attention is still under debate (Cave, Bush, & Taylor, 2010a, 2010b; Eimer, 2014; Eimer & Grubert, 2014; Jans, Peters, & De Weerd, 2010a, 2010b).

For internal attention, it has not yet been investigated whether the representations of objects presented at noncontiguous locations can be selected and protected, just like those of objects presented at contiguous locations. This is not just an interesting question in itself, but may also shed light on whether the effects of feature-based and spatial retrocues do indeed rely on different attentional mechanisms. The pronounced similarities between internal and external attention can be taken to suggest that internal feature-based and spatial attention might differ with respect to enhancing representations within the spatial layout of VWM, just as external feature-based and spatial attention differ with respect to enhancing perceptual processing across the visual field.

Rationale of the experiment

In two experiments, we investigated whether attention can selectively influence the contents of VWM operating on features just as well as on spatial locations. During the maintenance interval of a visual working memory task, a retrocue was presented that indicated two of the memorized items as being relevant. The efficacy of different types of spatial and feature-based retrocues was tested (see Fig. 1). In addition to a typical spatial retrocue (an octagram with blackened corners pointing toward two locations), we also presented a more symbolic spatial retrocue (numbers mapping onto two locations). Feature-based retrocues were a color retrocue (a blob the color of two of the memorized items) in the first experiment, and a shape retrocue (an outline of the shape of two of the memorized items) in the second experiment. To determine whether these feature-based and spatial retrocues relied on different attentional mechanisms and were not, in the case of feature-bases retrocues, simply (re)coded into spatial information, we examined whether they differed with respect to access to the representations of items presented at contiguous and noncontiguous locations. To this end, either two neighboring or two nonneighboring items were cued. It should be noted that an ongoing debate concerns the number of items that can be retroactively cued with resulting benefits: Whereas some studies have only observed benefits for cueing one item (e.g., Makovski & Jiang, 2007), others have also found benefits for cueing two items (e.g., Poch, Campo, & Barnes, 2014). This debate and the implications of the present study with respect to this issue are revisited more thoroughly in the Discussion section. To allow for the presentation of items spaced closely enough to be considered as neighboring or nonneighboring without exceeding mean VWM capacity, the task was lateralized. In each trial, participants were to memorize four items presented in one hemifield.

On the basis of the high similarity between external and internal attention, as well as the few previous studies reporting benefits for retrocues based on nonspatial information that we discussed above, we predicted overall retrocueing benefits for all retrocue types. Crucially, however, we expected to observe differences between the feature-based and spatial retrocues in the analysis of neighboring and nonneighboring cued items. Specifically, for feature-based retrocues we expected to observe retrocueing benefits irrespective of the cued items' spatial configuration—that is, independent of whether the items were neighboring or nonneighboring. For spatial retrocues, in contrast, we expected to observe large benefits for cueing neighboring items, but no or strongly attenuated benefits for cueing nonneighboring items. This pattern of results would corroborate the notion of internal feature-based and spatial attention mechanisms that operate in a manner similar to that of external feature-based and spatial attention.

Method

Participants

In all, 40 students from Philipps University Marburg participated in the experiments (Exp. 1: 16 female, seven male, mean age 22 years; Exp. 2: 13 female, four male, mean age 22 years), for which they received course credit or monetary compensation. All participants provided informed written consent, were naive to the purpose of the experiment, and had normal or corrected-to-normal visual acuity and color vision. Visual acuity and color vision were tested with the OCULUS Binoptometer 3 (OCULUS Optikgeräte GmbH, Wetzlar, Germany).

Apparatus

Participants were seated in a comfortable chair in a dimly lit and sound-attenuated room. Stimuli were presented on a 22-in. screen (1,680 × 1,050 pixels) placed at a distance of approximately 104 cm from the participants' eyes. Stimulus presentation and response collection were controlled by a Windows PC using E-Prime 2.0 software (Psychology

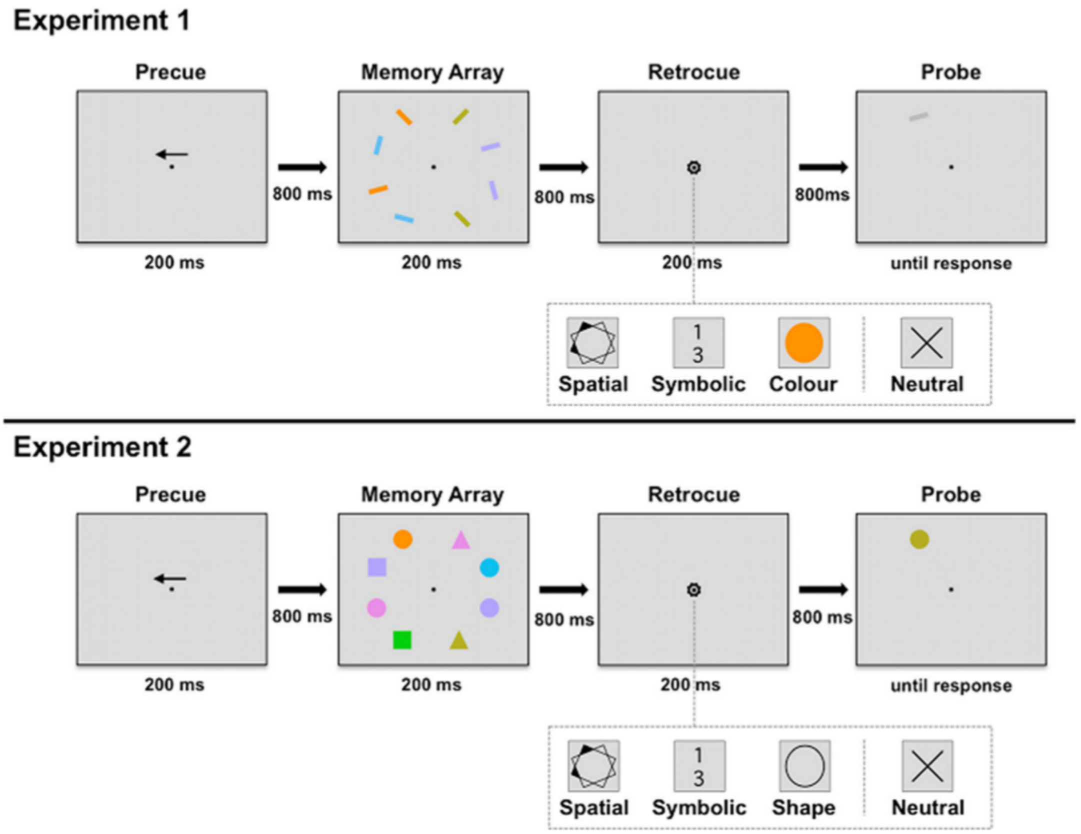

Fig. 1 Trial procedure and retrocue types for Experiments 1 (top) and 2 (bottom). A trial started with a precue presented above fixation for 200 ms, indicating the relevant hemifield for that trial. After an interval of 800 ms, a memory array consisting of eight items was presented for 200 ms. Participants were to remember the four orientations (Exp. 1) or colors (Exp. 2) of the items in the indicated hemifield. After another interval of 800 ms, the retrocue was presented. This retrocue was either informative, indicating two of the previously presented memory items as being task-relevant, or neutral ("X"), providing no information as to the task - relevance of specific items. Three different informative retrocue types were presented in each experiment. The spatial retrocues were octagrams with two blackened corners pointing to two locations of previously presented memory items. Symbolic retrocues consisted of two numbers mapping onto two of the four spatial locations in each hemifield (1 to 4, from top to bottom). These two types of spatial retrocues were identical in both experiments. The feature-based retrocue was a blob of the color (Exp. 1) or an outline of the shape (Exp. 2) of two of the previously presented memory items. After an interval of 800 ms, a probe item was presented at one of the memory item locations. Participants were to indicate whether this probe item was of the same orientation (Exp. 1) or color (Exp. 2) as the memory item that had previously been presented at that location. In trials with an informative retrocue, one of the two items indicated by the retrocue was probed. In trials with a neutral retrocue, one of the initial four memory items was tested

Software Tools, Inc.). Participants responded by pressing buttons on the back of a gamepad (Microsoft SideWinder USB).

Stimuli and procedure

All stimuli were presented against a gray background. There were eight fixed locations for the items in the memory array—four in each hemifield, and two in each quadrant. The memory items were arranged on an imaginary circle with a radius of approximately 4.68° of visual angle. They subtended an area of 1.10° × 0.28° of visual angle. The distance from the center of one item to the next was 3.31° of visual angle for neighboring items within one hemifield. The distance between two items that were next to each other but on opposite sides of the vertical midline was 4.68° of visual angle.

In Experiment 1, the orientations of the memory items were randomly chosen from a set of six orientations (15°, 45°, 75°, 105°, 135°, and 165°). The orientation of the probe item was either identical to the orientation of the memory item that had previously been presented at that location (on match trials) or was randomly chosen from the remaining set of orientations (on nonmatch trials). The colors of the memory items were chosen from a set of six colors (blue, green, lilac, ochre, orange, and pink). Two pairs of memory items in each hemifield were of the same color. The probe item was always presented in gray, and the colors of the memory and probe items were isoluminant.

In Experiment 2, the colors of the memory items were randomly chosen from a set of seven isoluminant colors (blue, green, ochre, orange, pink, red, and violet). A color could appear no more than once in each hemifield. The color of the probe item was either identical to the color of the memory item that had previously been presented at that location (on match trials) or was randomly chosen from the remaining set of colors (on nonmatch trials). As in Experiment 1, the memory and probe items were isoluminant. The shapes of the memory items were chosen from a set of three shapes (circles, squares, and triangles). Two pairs of memory items in each hemifield were of the same shape. The probe item was always of the same shape as the memory item that had previously been presented at the indicated location.

The precue subtended an area of 1.10° × 0.28° of visual angle. The neutral, spatial, color, and shape retrocues were 1.1° × 1.1° of visual angle in size, and the symbolic retrocue was 1.1° × 2.68° of visual angle in size. The fixation dot subtended an area of 0.02° of visual angle.

The procedure is illustrated in Fig. 1. A trial started with the presentation of a precue (an arrow) just above the fixation dot for 200 ms, which pointed toward the left or right, indicating the relevant hemifield for the trial. After an interval of 800 ms, a memory array was presented. This memory array consisted of eight memory items, and participants were asked to memorize the four items in the relevant hemifield. Participants had to remember the orientations of the items in Experiment 1, and the colors of the items in Experiment 2. After an interval of 800 ms, either an informative or a neutral retrocue was presented. An informative retrocue validly indicated two of the memory items. In Experiment 1, this was either a spatial retrocue (an octagram with two blackened corners pointing toward two locations), a symbolic retrocue (two numbers mapping onto two locations, with the locations being numbered from 1 to 4 from top to bottom in each hemifield) or a color retrocue (a blob the same color as two of the memory items). In Experiment 2, the spatial and symbolic retrocues were the same as in Experiment 1, and the feature-based retrocue was a shape retrocue (an outline the same shape as two of the memory items) instead of a color retrocue. In both experiments, there were also neutral trials, in which a noninformative neutral retrocue (an X) was presented. After another interval of 800 ms, a probe item was presented at one of the memory item locations, and participants were to indicate whether this probe item had the same orientation (Exp. 1) or color (Exp. 2) as the memory item that had previously been presented at that location, or a different one. In 50 % of all trials, a change in orientation or color occurred. In trials with an informative retrocue, the probe item was always presented at one of the locations of the two cued memory items. In neutral trials, the probe item was presented at one of the four memory item locations. The probe item was present until response, but participants were encouraged to respond quickly. They pressed a button with their left or right index finger, and the response assignment was balanced across participants.

Design

Testing took place in three (Exp. 1) or two (Exp. 2) sessions on separate days, with no more than two days between sessions. The first session or the first two sessions, respectively, were shorter training sessions, and these data were not entered into the analyses. The main experiments consisted of 1,152 trials, with 384 trials for each retrocue type (spatial, symbolic, and color/shape), organized in blocks of 32 trials each. Retrocue type was varied blockwise, with a change in retrocue type every three blocks. The order in which the retrocue types were presented was balanced across participants. Retrocue information (50 % informative, 50 % neutral) was varied trialwise. Thus, neutral retrocue trials were identical but interleaved with different types of informative retrocues. In half of all trials with informative retrocues, the two cued items were items that had been presented at neighboring locations (at Locations 1 and 2, 2 and 3, or 3 and 4, with locations numbered from top to bottom in each hemifield), and in the other half, the cued items had been presented at nonneighboring locations (at Locations 1 and 3, 1 and 4, or 2 and 4).

Data analyses

Trials with excessively long reaction times (>2.5 *SD*s from the mean reaction time, calculated separately for each participant) were excluded from further analysis (on average, 2.8 % of all trials in both experiments). For each experimental condition, accuracy in percent, mean reaction time, and an index of sensitivity (*d*-prime [*d'*]) were calculated. For reaction times, only correct responses were included. The *d'* scores were calculated as $d' = z(\text{hit rate}) - z(\text{false alarm rate})$.

Repeated measures analyses of variance (ANOVAs) with the factors Retrocue Type (spatial, symbolic, and color) and Retrocue Information (informative and neutral) were computed, followed by pairwise comparisons when appropriate. Only the significant comparisons are reported. In addition, one-tailed *t* tests comparing performance for informative retrocues indicating neighboring and nonneighboring items against performance in the respective neutral conditions were computed, separately for each retrocue type.

Results

Experiment 1

The results of Experiment 1 are illustrated in Figs. 2 and 3, top panels. A significant main effect of retrocue type was observed for all measures [accuracy, $F(2, 44) = 5.76$, $p = .006$, $\eta_p^2 = .21$; reaction time, $F(2, 44) = 5.51$, $p = .007$, $\eta_p^2 = .20$; d', $F(2, 44) = 3.90$, $p = .027$, $\eta_p^2 = .15$]. Performance was best for color retrocue blocks, followed by spatial and symbolic

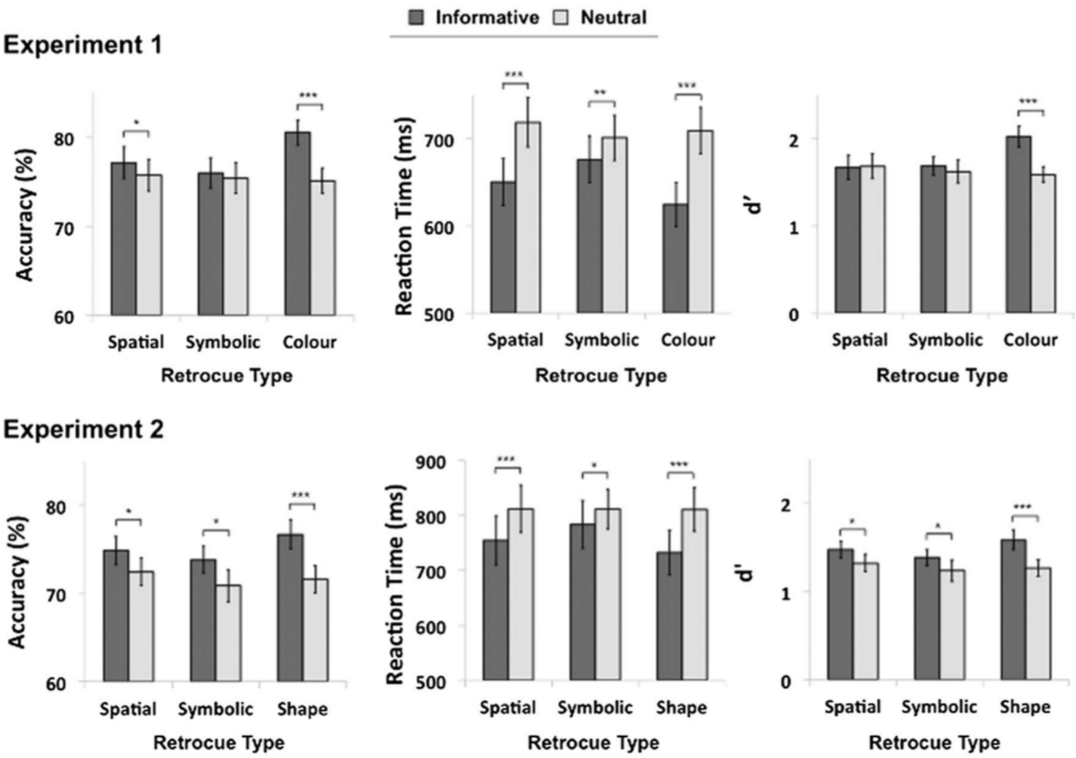

Fig. 2 Overall retrocueing benefits in Experiments 1 (top) and 2 (bottom). For each experiment, accuracy in percent (left column), mean reaction time (middle column), and *d′* (right column) for trials with informative (dark gray) and neutral (light gray) retrocues are shown separately for the three different retrocue types (spatial, symbolic, and color/shape). Error bars show the standard errors of the means, and asterisks mark significant retrocueing benefits—that is, significant differences between informative and neutral retrocues. $^{*}p < .05$; $^{**}p < .01$; $^{***}p < .001$

retrocues. Pairwise comparisons revealed that performance for color retrocues was significantly better than performance for spatial retrocues (reaction time, –17.71 ± 7 ms, $p = .035$) and for symbolic retrocues (accuracy, 2.10 % ± 0.6 %, $p = .13$; reaction time, –21.81 ± 8 ms, $p = .024$; *d′*, 0.15 ± 0.1, $p = .035$). Importantly, performance was significantly better in informative retrocue trials than in neutral retrocue trials across retrocue type conditions, as was shown by a significant main effect of retrocue information [accuracy, $F(1, 22) = 21.46$, $p < .001$, $\eta_p^2 = .49$; reaction time, $F(1, 22) = 183.56$, $p < .001$, $\eta_p^2 = .89$; *d′*, $F(1, 22) = 16.14$, $p = .001$, $\eta_p^2 = .42$]. Thus, there were significant benefits for informative as compared to neutral retrocues. Significant interactions [accuracy, $F(2, 44) = 12.01$, $p < .001$, $\eta_p^2 = .35$; reaction time, $F(2, 44) = 18.31$, $p < .001$, $\eta_p^2 = .45$; *d′*, $F(2, 44) = 8.24$, $p = .001$, $\eta_p^2 = .27$] revealed differences in the magnitudes of these benefits for informative as compared to neutral trials between retrocue type conditions. As is shown in Fig. 2 (top), the difference between informative and neutral retrocue trials was largest for color retrocues, followed by spatial and symbolic retrocues. Pairwise comparisons revealed significant differences between the retrocueing benefits for color retrocues and symbolic retrocues (accuracy, 4.85 % ± 1.3 %, $p = .003$; reaction time, –60.0 ± 12 ms, $p < .001$; *d′*, 0.37 ± 0.1, $p = .029$) and for color retrocues and spatial retrocues (accuracy, 4.02 % ± 0.9 %, $p = .001$; *d′*, 0.44 ± 0.1, $p = .003$), as well as a difference between spatial retrocues and symbolic retrocues in terms of reaction times (–43.82 ± 10 ms, $p = .001$).

In a second step, we examined the retrocueing benefits for neighboring as well as for nonneighboring cued items (Fig. 3). We found significant retrocueing benefits for neighboring cued items for all retrocue types and all measures [*spatial*: accuracy, $t(22) = 4.98$, $p < .001$; reaction time, $t(22) = –8.64$, $p < .001$; *d′*, $t(22) = 2.7$, $p = .013$; *symbolic*: accuracy, $t(22) = 2.84$, $p = .01$; reaction time, $t(22) = –3.64$, $p = .001$; *d′*, $t(22) = 4.05$, $p = .001$; *color*: accuracy, $t(22) = 9.98$, $p < .001$; reaction time, $t(22) = –11.01$, $p < .001$; *d′*, $t(22) = 6.72$, $p < .001$]. For nonneighboring cued items, in contrast, significant retrocueing benefits for all measures were only observed with color retrocues [accuracy, $t(22) = 3.16$, $p = .005$; reaction time, $t(22) = –11.04$, $p < .001$; *d′*, $t(22) = 6.72$, $p < .001$]. In terms of reaction time, there was also a retrocueing benefit for spatial retrocues [$t(22) = –5.05$, $p < .001$].

Experiment 2

The results of Experiment 2 are illustrated in Figs. 2 and 3, bottom panels. The same analyses were conducted as for

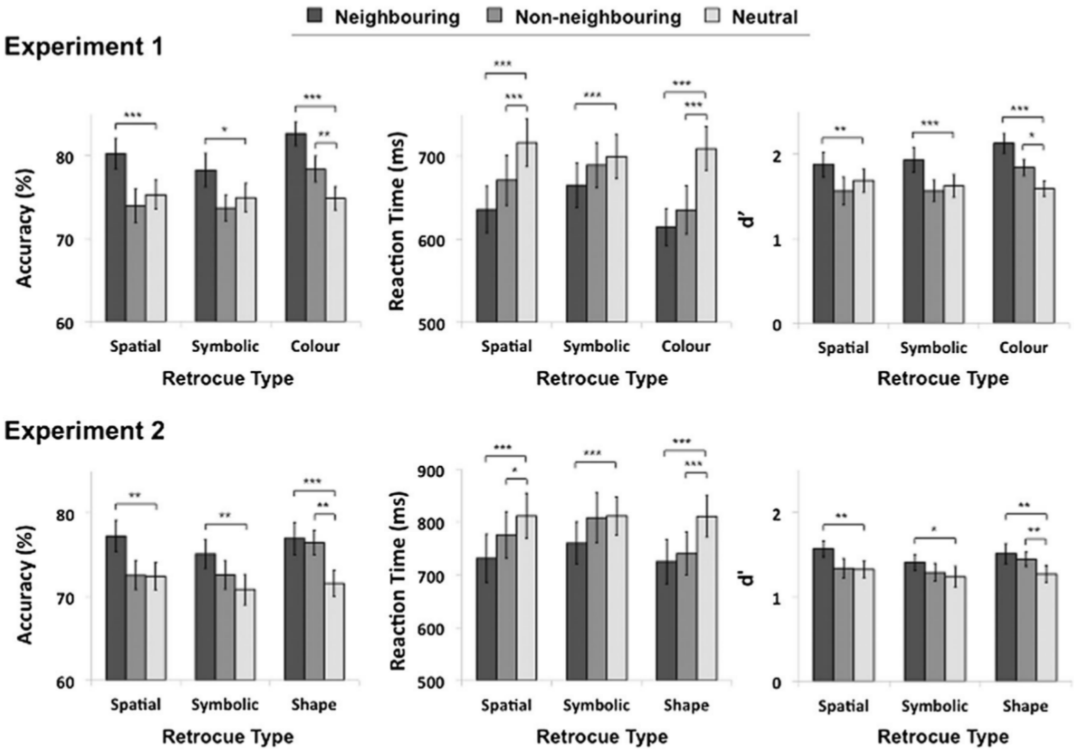

Fig. 3 Retrocueing benefits for neighboring and nonneighboring items in Experiments 1 (top) and 2 (bottom). For each experiment, accuracy in percent (left column), mean reaction time (middle column), and *d'* (right column) for retrocues indicating neighboring (dark gray) or nonneighboring (medium gray) items and for neutral retrocues (light gray) are shown separately for the three different retrocue types (spatial, symbolic, and color/shape). Error bars show the standard errors of the means, and asterisks mark significant retrocueing benefits—that is, significant differences between informative and neutral retrocues. $^{*}p < .05$; $^{**}p < .01$; $^{***}p < .001$

Experiment 1. Repeated measures ANOVAs with the factors Retrocue Type (spatial, symbolic, and shape) and Retrocue Information (informative and neutral retrocues) revealed significant main effects of retrocue type for accuracy [$F(2, 32) = 3.94$, $p = .029$, $\eta_p^2 = .20$] and *d'* [$F(2, 32) = 3.3$, $p = .048$, $\eta_p^2 = .17$], with better performance for shape than for spatial and symbolic retrocues. Pairwise comparisons revealed significant differences between shape and symbolic retrocues (accuracy, 1.80 % ± 0.6 %, $p = .026$; *d'*, 0.12 ± 0.04, $p = .039$). In addition, across retrocue type conditions, performance was better in informative retrocue trials than in neutral retrocue trials [accuracy, $F(1, 22) = 38.07$, $p < .001$, $\eta_p^2 = .70$; reaction time, $F(1, 22) = 30.55$, $p < .001$, $\eta_p^2 = .66$; *d'*, $F(1, 22) = 32.04$, $p < .001$, $\eta_p^2 = .67$]. The interaction between retrocue type and retrocue information only reached significance for reaction times [$F(2, 32) = 8.07$, $p = .001$, $\eta_p^2 = .34$]. The benefit of informative as compared to neutral retrocues was larger for shape retrocues than for spatial and symbolic retrocues. The difference between the benefits for shape and symbolic retrocues was significant (50.70 ± 12 ms, $p = .002$).

In addition, we observed significant retrocueing benefits for neighboring cued items for all retrocue types and all measures [*spatial*: accuracy, $t(16) = 2.86$, $p = .006$; reaction time, $t(16) = –5.98$, $p < .001$; *d'*, $t(16) = 3.5$, $p = .002$; *symbolic*: accuracy, $t(16) = 3.49$, $p = .002$; reaction time, $t(16) = –4.47$, $p < .001$; *d'*, $t(16) = 2.49$, $p = .012$; *shape*: accuracy, $t(16) = 4.62$, $p < .001$; reaction time, $t(16) = –7.45$, $p < .001$; *d'*, $t(16) = 3.54$, $p < .002$]; see Fig. 3. For nonneighboring cued items, as in Experiment 1, significant retrocueing benefits for all measures were only observed for feature-based retrocues—that is, for the shape retrocues [accuracy, $t(16) = 3.54$, $p = .002$; reaction time, $t(16) = –6.18$, $p < .001$; *d'*, $t(16) = 3.10$, $p = .004$]. In terms of reaction times, there was also a significant retrocueing benefit for spatial retrocues [$t(16) = –2.38$, $p = .015$].

Discussion

The present experiments demonstrate that attention can select representations maintained in VWM not only on the basis of spatial location, but also on the basis of features of the represented objects. Retrocueing benefits for informative spatial and symbolically spatial retrocues, relative to a neutral retrocue, were observed, as well as for two different types of feature-based retrocues. Not only was retrocueing an object's feature just as advantageous as retrocueing an object's location, but when there were differences in the magnitudes of the observed benefits, the benefit was even larger for feature-based than for spatial retrocues. This was the case when color was the feature used for cueing (Exp. 1) and, to a lesser degree, also observed when object shape was the cued feature (Exp. 2). It should be noted that the number retrocues, for which a previous study had not observed benefits (Berryhill et al., 2012), yielded significant but relatively small benefits. This may be the result of the symbolic nature of number retrocues, which rely on an experimenter-defined mapping of numbers onto locations. Therefore, these retrocues might require more time or effort to be decoded than do more intuitive and overlearned cues, such as the blackened corners of the spatial retrocues, which resemble arrowheads. Some of the experimental parameters, such as the addition of a training session, a blockwise variation of retrocue type, and a longer interval between retrocue and probe item, might thus explain the seemingly divergent findings with respect to the efficacy of number retrocues. Interestingly, effects of number cues have also been reported to be smaller than the effects of other cues, especially arrow cues, for external attention (e.g., Olk, Tsankova, Petca, & Wilhelm, 2014 ; Ristic & Kingstone, 2006).

The smaller overall benefits for the two spatial retrocues than for the feature-based retrocues can be accounted for by differences in the benefits for neighboring and nonneighboring cued items. Whereas there were benefits for both neighboring and nonneighboring cued items for the two feature-based retrocues, a benefit in performance for the two spatial retrocues was only found for neighboring cued items. Thus, the attentional mechanisms underlying the effects of spatial and feature-based retrocues differ with respect to their access to representations of objects presented at contiguous and noncontiguous locations. These results support the idea that these attentional mechanisms are qualitatively different. Specifically, they suggest that, just as in the perceptual domain, there is a distinction between feature-based and spatial attentional selection at the mnemonic level. Whereas internal feature-based attention enhances representations with behaviorally relevant features across the spatial layout of VWM, internal spatial selection of noncontiguous representations appears to be harder to realize, if not impossible.

The present findings support the notion of similar external and internal mechanisms of feature-based and spatial attentional selection, and add to a growing body of evidence demonstrating a high degree of similarity between external and internal attention. Similarities have been observed with respect to behavioral consequences and neural networks (e.g., Griffin & Nobre, 2003; Nee & Jonides, 2009; Tamber-Rosenau et al., 2011). In light of this evidence, one might question whether making a distinction between external and internal attention is appropriate at all. However, there are also notable differences between the two domains of attentional orienting. For example, neuroimaging studies have found an additional involvement of certain medial and lateral prefrontal areas and stronger activations in parietal regions when the focus of attention is controlled within VWM (Nee & Jonides, 2009; Nobre et al., 2004; Tamber-Rosenau et al., 2011). Moreover, internal attention has also been shown to exhibit distinct behavioral characteristics: Unlike external shifts of attention, internal shifts of attention appear not to be influenced by the initial physical distance of the encoded objects, and beyond a certain threshold time, additional time for internal shifts does not yield additional benefits (Tanoue & Berryhill, 2012).

In addition, as was pointed out by Chun et al. (2011), a distinction between internal and external attention is useful for organizing and structuring research and findings, and it does not necessarily imply that the mechanisms are truly separate. Importantly, in Chun et al.'s taxonomy, they place working memory at the interface of internal and external attention. The content that attention operates on in VWM is clearly internal: These are representations of information that is no longer physically present in the outside world. However, there is a substantial overlap between VWM and (external) attention (Awh & Jonides, 2001; Gazzaley & Nobre, 2012), and it has been suggested that the two mechanisms might share an underlying resource (Anderson, Vogel, & Awh, 2013; Kiyonaga & Egner, 2013). Their linkage is, for instance, indicated by evidence showing that VWM's content influences the deployment of external attention (e.g., Feldmann-Wüstefeld & Schubö, 2015; Olivers, Peters, Houtkamp, & Roelfsema, 2011; Soto, Heinke, Humphreys, & Blanco, 2005).

Thus, internal and external attention exhibit both commonalities and differences, and the investigation of the relationship between the two domains of attentional orienting continues to be particularly important in order to clarify in how far these attentional mechanisms are distinct. The present experiments contribute to our understanding of the overlap of perceptual and mnemonic processing by showing that internal feature-based and spatial attentional selection mechanisms resemble the ways that features and spatial locations are selected in the external world.

The units of VWM: Objects, features, or both?

We perceive and remember our visual surroundings in terms of objects and not as an assemblage of features, and the unit for storage in VWM is predominantly considered to be integrated objects rather than individual features (Cowan, 2001; Luck & Vogel, 1997; Luria & Vogel, 2011). The present findings are consistent with such an object-based account of VWM. Participants were instructed to remember one feature of the objects (orientation in Exp. 1, color in Exp. 2), and not the other features that were used to cue specific items. Nevertheless, these cued features could be used to weigh the items with respect to their behavioral relevance. Thus, by accessing one feature of an object, memory for another feature of that object could be improved. It is conceivable that in the present experiments, the features used to cue specific items were automatically encoded and maintained along with the to-be-memorized features. In this context, it should also be pointed out that performance in a change detection task such as the one used here always depends on one other feature that participants are almost never explicitly instructed to memorize and that is not tested, but that appears to be available nonetheless: location. Indeed, there is evidence that relative location is encoded along with information about object identity (Olson & Marshuetz, 2005). Alvarez and Cavanagh (2004) suggested that an obligatory set of features, including but not limited to location information, might form an object representation. Moreover, it has been shown that even task-irrelevant features are automatically encoded along with the relevant features of objects, and that only subsequent maintenance is under voluntary control (Marshall & Bays, 2012; Xu, 2010). Given that both location and the respective feature used for retrocueing were relevant for the task at hand, it seems reasonable to assume that, after an initial automatic encoding, these features were maintained along with the tested feature in an object-based manner. Object-based storage in VWM could also explain how a retrocue relying on one feature can yield a benefit in memory for another feature of the particular object, since it has been shown that attending to one feature of an object enhances the neural representation not only of that feature, but also of other features of the object (O'Craven, Downing, & Kanwisher, 1999).

Recently, an alternative framework to object-based models has been proposed, according to which the representational units of VWM are not objects, but features (Fougnie & Alvarez, 2011; see also Wheeler & Treisman, 1993). Fougnie and Alvarez observed that reports for different features of an object were largely independent, meaning that even when one feature was unknown, another feature of the same object could be successfully reported. They postulated that VWM is organized in self-sustaining representations that may fail independently for each feature, and that the independence of the maintained features is determined by the degree of overlap in their neural coding during perception. The memory representations for color and orientation, and also for shape and color, would consequently be largely independent, which is hard to reconcile with the present findings. Similarly, Rajsic and Wilson (2014) have suggested a location-based representational organization, with nonspatial features nested within locations. Such a model, according to which representations are indexed by location, would seem to imply that a spatial code is necessary for the attentional selection of information in VWM. Thus, it cannot account for our findings indicating that a nonspatial feature of an object can be accessed just as well via another nonspatial feature.

Although our findings support an object-based organization of VWM, they might have been influenced by task-specific demands. Consistent with the general notion of a high flexibility of VWM, and offering a possible explanation for the divergent findings with respect to its basic units, a recent study by Vergauwe and Cowan (2015) suggests that the representational units in VWM might also be flexible to some degree. Vergauwe and Cowan examined whether performance in a VWM task depended on the number of objects, the number of features, or both. Crucially, they explicitly either encouraged or discouraged the use of binding information through the instructions, and presented test probes either as integrated objects or as independent features. They found that the testing situation affected the unit for retrieval from VWM, in that it could result in a stronger emphasis on either the features or the objects. When the representation of objects was stressed by encouraging binding and presenting integrated object probes, retrieving multiple features did not take longer than retrieving a single feature. The authors concluded that the unit of VWM may not be fixed, and that relatively small changes in the experimental details can influence which unit is favored. The present experiments, one might argue, emphasized the coding of objects, in that the binding of a location and the to-be-memorized feature was required to perform the memory task itself, as well as to make use of the spatial retrocues. In order to incorporate the feature cue, this feature needed to be integrated with both the to-be-memorized feature and the location.

How many representations in VWM can be selected?

Although a number of state-based models of VWM have posited different activation states of representations that are established by the deployment of attention (LaRocque, Lewis-Peacock, & Postle, 2014), these models differ in their conceptualizations of how many items or elements can be selected. It has been proposed that only one item can be in the focus of attention (Oberauer, 2002; Olivers et al., 2011), thereby ensuring heightened processing efficiency for the selected information (Oberauer & Bialkova, 2009). Alternatively, the focus of attention might be able to encompass multiple items, up to its approximate limit of four (Cowan et al., 2005), allowing for a higher degree of flexibility and adjustability of the focus according to different task demands. Empirical evidence has been obtained for both a narrow focus of attention, of only one item (Garavan, 1998; Makovski & Jiang, 2007; Oberauer & Bialkova, 2009), and a broader focus of attention that can grasp multiple items (Cowan, 2011; Heuer & Schubö 2016, manuscript submitted for publication; Poch et al., 2014).

In the present experiments, participants had to select two representations in VWM, which yielded a benefit in memory performance relative to when no subset of representations was selected. Even though the retrocueing benefit is now well-established, the observation of such a benefit for multiple cued items is not trivial, given that it is still being debated how many elements can be selected from VWM at the same time. The overall benefits observed for informative retrocues support the notion that multiple items can be in the focus of attention at the same time. An even stronger indication that both cued items were indeed attentionally selected is provided by the analyses of performance for neighboring and nonneighboring cued items. Several alternative explanations for the observation of benefits for cueing multiple items do not imply a multiple-item focus of attention, as we discuss below. These alternative explanations, however, are rendered unlikely by the effects of the different spatial configurations of the two cued items.

First, it is possible that in fact only one item was selected, although two items were cued. This might still have resulted in better performance than on trials with a neutral retrocue, seeing that on a certain proportion of trials the selected item would have been tested. But if only one of the two cued items was in the focus of attention, it should not have made any difference for the observed benefits whether the cued items had been presented at contiguous or noncontiguous locations. Such a difference, however, is exactly what we found for the two spatial retrocues: Whereas there were significant benefits for items at neighboring locations, no benefits were observed for items at nonneighboring locations.

On a related note, one might argue that a single-item focus was rapidly shifted from one cued item to the other. This might have resulted in a reduction or obliteration of benefits for items that had been presented farther apart (i.e., nonneighboring items), because the time in-between the presentation of the retrocue and the probe item might not have sufficed to shift attention to the second item.[1] Importantly, however, this should have been the case not only for spatial retrocues, but also for feature retrocues, for which benefits for nonneighboring cued items were observed. Moreover, it has been shown that the distance between objects at encoding does not affect the time it takes to shift internal attention between the respective representations (Tanoue & Berryhill, 2012).

A third alternative explanation is that the two cued items were chunked, and thus effectively processed as one element (see also Oberauer & Bialkova, 2009). However, there is no obvious reason why chunking nonneighboring items would have been possible with feature-based retrocues, but not with spatial retrocues. Even though the feature-based retrocues might have highlighted commonalities between the two cued items—that is, their common color or shape—thereby enhancing the process of chunking, this certainly does not account for the absolute lack of benefits for nonneighboring cued items in trials with spatial retrocues. Instead, the results indicate that the two cued items were treated as two elements that were selected into a multiple-item focus of attention.

We would like to point out that the contradictory conclusions with respect to the number of items that can be in the focus of attention within VWM have been reached with very different paradigms, which may account for the divergent results. For example, a change detection task involving exogenous retrocues and a number of memory items beyond working memory capacity (Makovski & Jiang, 2007) and an arithmetic task requiring operations involving serially and centrally presented digits (Oberauer & Bialkova, 2009) might pose very different demands on attentional mechanisms. On the basis of the present experiments, we cannot rule out that in some situations only one element from working memory might be attentionally accessed. But our findings strongly support the notion that under specific circumstances the internal focus of attention can encompass multiple representations.

Conclusions

Attentional selection in VWM can operate on different types of information, which can be used to update the contents of VWM according to the behavioral relevance of specific objects. This demonstrates a high flexibility of the working memory system with respect to making use of whatever information is available, ensuring that limited storage capacity is used efficiently. The mechanisms of internal feature-based and spatial attention resemble the respective mechanisms in the external domain, in that only feature-based attention can reliably select and enhance noncontiguous representations throughout the spatial layout of VWM.

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[1] On the basis of findings on the time course of attention in the perceptual domain—for example, in visual search and attentional dwell time tasks (e.g., Moore, Egeth, Berglan, & Luck, 1996; Woodman & Luck, 2003)—the interval of 800 ms should have been sufficient to deploy attention to two locations. One might argue that estimates for external attention do not necessarily apply to the mnemonic domain, but retrocueing benefits have even been observed when the time to shift internal attention to one representation was less than 150 ms (Tanoue & Berryhill, 2012).

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Study III

Different cortical mechanisms for spatial vs. feature-based attentional selection in visual working memory

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Abstract

The limited capacity of visual working memory necessitates attentional mechanisms that selectively update and maintain only the most task-relevant content. Psychophysical experiments have shown that the retroactive selection of memory content can be based on visual properties such as location or shape, but the neural basis for such differential selection is unknown. For example, it is not known if there are different cortical modules specialized for spatial versus feature-based mnemonic attention, in the same way that has been demonstrated for attention to perceptual input. Here, we used transcranial magnetic stimulation (TMS) to identify areas in human parietal and occipital cortex involved in the selection of objects from memory based on cues to their location (spatial information) or their shape (featural information). We found that TMS over the supramarginal gyrus (SMG) selectively facilitated spatial selection, whereas TMS over the lateral occipital cortex selectively enhanced feature-based selection for remembered objects in the contralateral visual field. Thus, different cortical regions are responsible for spatial vs. feature-based selection of working memory representations. Since the same regions are involved in attention to external events, these new findings indicate overlapping mechanisms for attentional control over perceptual input and mnemonic representations.

1. Introduction

Visual working memory (VWM) allows us to maintain and manipulate visual information over short periods of time for various cognitive and motor tasks. However, this critical function has a highly limited capacity (Luck & Vogel, 1997; Zhang & Luck, 2008). As a result of this limitation, it is important for the brain to continuously and selectively update the contents held in VWM, thereby improving memory for some objects at the expense of others (e.g., Kuo, Stokes, & Nobre, 2012; Zokaei, Ning, Manohar, Feredoes, & Husain, 2014). Further, in order to achieve the flexibility required for different tasks, this selection process must operate in different qualitative domains, such as spatial versus featural information (Heuer & Schubö, 2016; Li & Saiki, 2014; Pertzov, Bays, Joseph, & Husain, 2013). However, the neural mechanisms used to deploy such differential selection are unknown at this time.

By comparison, much more is known about selective attention in perception. In particular, it has been shown that spatial and feature-based perceptual attention have different behavioral consequences and different neural mechanisms (e.g., Carrasco, 2011; Greenberg, Esterman, Wilson, Serences, & Yantis, 2010; Maunsell & Treue, 2006; Schenkluhn, Ruff, Heinen, & Chambers, 2008). Perceptual and mnemonic attentional selection have been shown to exhibit many commonalities, but there are also notable differences in terms of behavioral signatures (e.g., Tanoue & Berryhill, 2012) and cortical mechanisms (Nee & Jonides, 2009; Nobre et al., 2004; Tamber-Rosenau, Esterman, Chiu, & Yantis, 2011). Therefore, one cannot assume that mnemonic and perceptual attention share the same feature-specific cortical mechanisms.

In the present study, we used structural magnetic resonance imaging (MRI)-guided, on-line repetitive transcranial magnetic stimulation (rTMS) to test whether spatial and feature-based attention to remembered visual objects can be dissociated based on the site of cortical stimulation. On-line TMS can transiently disrupt activity in a localized brain region, thereby establishing a causal, spatiotemporal link between this region and cognitive functions engaged at that point in the task (e.g., Bolognini & Ro, 2010; Hallett, 2000). In a change detection task, participants were required to remember the colors of three differently shaped items, and then report whether there was a color change for one of the items. The items were presented either in the left or in the right visual hemifield to allow for an investigation of a potential lateralization with respect to the stimulated right hemisphere. A lateralization of attentional selection in VWM has previously been observed in electrophysiological studies (Griffin & Nobre, 2003; Myers, Walther, Wallis, Stokes, & Nobre, 2015; Poch, Campo, & Barnes, 2014). The right hemisphere was chosen for stimulation, because the attentional network has often been shown to be right-hemisphere dominant (e.g., Chang et al., 2013; Corbetta & Shulman, 2002; Thiebaut de Schotten et al., 2011). During the retention interval, a so-called 'retrocue' was presented, that is, a cue indicating specific previously presented items as more behaviorally relevant than others. This retrocue indicated the upcoming test item either by its location (spatial attention) or by its shape (feature-based attention). Based on previous studies (Heuer & Schubö, 2016; Li & Saiki, 2014; Pertzov et al., 2013), we expected a general improvement in performance in cued compared to neutral control trials for both feature-based and spatial retrocues. We then selectively targeted the cortical mechanisms for spatial vs. feature-based attentional selection by delivering a short train of three TMS pulses to the right supramarginal gyrus (SMG) or the right lateral occipital cortex (LO) during presentation of the retrocue. These areas were chosen based on what is known about their roles in perceptual attention. Whereas parietal SMG has been implicated in the control of spatial attention (Chambers, Stokes, & Mattingley, 2004; Schenkluhn et al., 2008), extrastriate visual cortex is involved in feature-based attention (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen , 1991; Murray & Wojciulik, 2004; Schoenfeld et al., 2007), with LO playing a specific role in the representation of object shape (Grill-Spector, Kourtzi, & Kanwisher, 2001; Kim, Biederman, & Juan, 2011; Kourtzi & Kanwisher, 2000). If these areas play similar roles in the differential selection of mnemonic representations, stimulation of SMG vs. LO during the cue presentation should produce differential effects on attentional selection based on location vs. shape, thus dissociating spatial and feature-based attention in VWM at the cortical level.

2. Materials & Methods

2.1 Participants

Eleven volunteers (seven females; mean age: 27 years, SD = 6 years; two left-handed) participated in the experiment. All participants were in good health, had normal or corrected-to-normal visual acuity and color vision and, according to self-report, no known contraindications to TMS. Participants provided informed written consent before the experiment but were otherwise naive to the purpose of the study. The procedures were approved by the York University Human Participants Review Subcommittee and in accordance with the Declaration of Helsinki.

2.2 Apparatus

Participants were seated in a dimly lit room, facing a CRT monitor (19”, frame rate 85Hz) placed at a distance of approximately 100 cm from their eyes. During the experiment, their head was fixed in an upright position centrally to the monitor by individual dental impressions (bite bars). Participants responded by pressing two buttons on a keyboard placed on a table in front of them with the index and middle finger of their right hand. Stimulus presentation and response collection were controlled by a Windows PC using E-Prime 2.0 software (Psychology Software Tools, Inc.).

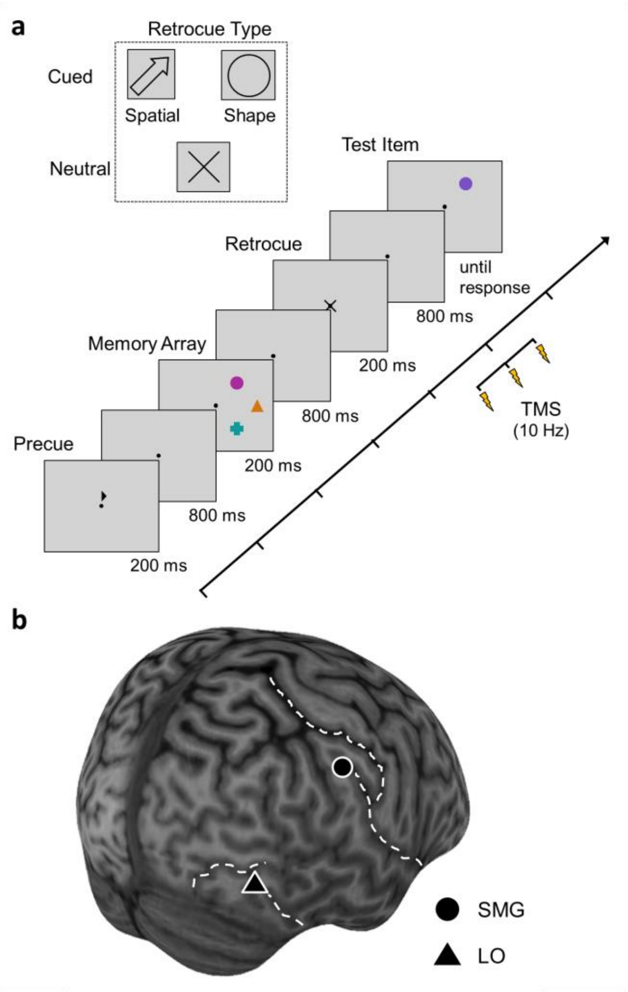

Figure 1. Task and TMS protocol. (a) A trial for the right hemifield. Participants memorized colors of the items in the memory array, and indicated whether the test item had the same color as the item previously presented at that location. In cued trials, the retrocue indicated the test item by its location or shape. In neutral trials, the retrocue was uninformative. In TMS conditions, a train of three pulses was applied during retrocue presentation. The first pulse was delivered 100 ms after retrocue onset. (b) Location of TMS sites SMG and LO in the right hemisphere of one participant. Dashed lines indicate the sulci that were used to identify the sites.

2.3 Stimuli and Task

All stimuli were presented against a grey background and participants were instructed to maintain fixation on a central dot (0.8° of visual angle) throughout the experimental trials. Our visual stimuli and task are most easily described in terms of the temporal sequence of steps illustrated in Figure 1a:

Step 1: A trial started with the presentation of a precue (an arrowhead subtending 0.94° x 0.50°) above the fixation dot for 200 ms, which pointed towards the left or right, thereby indicating the relevant visual hemifield for that trial. This precue allowed participants to selectively allocate attention to the correct hemifield, facilitating the upcoming encoding process and reducing the likelihood of eye movements toward transiently presented memory items.

Steps 2 and 3: After an interval of 800 ms, the memory array was presented, which consisted of three memory items in the relevant hemifield. Participants were instructed to memorize the colors of these items. Memory items subtended an area of 1.10° of visual angle and were arranged on an imaginary circle with a radius of 4.96° with a distance of 3.58° between items. The colors of the memory items were randomly chosen from a set of seven colors (magenta, violet, blue, turquoise, green, orange, and red) with the restriction that no two memory items could be of the same color. The number of memory items was close to the capacity limit of VWM (e.g., Luck & Vogel, 1997), and the colors were adjusted so that baseline performance was within the optimal zone of difficulty for TMS effects on working memory (see Prime, Vesia, & Crawford, 2008, 2010). The shapes of the memory items were chosen from a set of four shapes (circle, cross, square, and triangle). On a given trial, all memory items were of different shapes. All 24 possible combinations of locations and shapes were presented equally often and in a randomized order.

Steps 4 and 5: After 800 ms, the retrocue (0.83°) was presented for 200 ms (see Figure 1a, upper panel for details of the retrocue stimulus appearance). In cued trials, the retrocue indicated one of the memorized items by either its location (spatial retrocue) or its shape (shape retrocue). Participants were informed that this was the item that would be tested at the end of the trial. In neutral trials, a non-informative retrocue was presented (an “X”).

Steps 6 and 7: After another interval of 800 ms, the test item was presented at one of the memory item locations, and participants had to indicate whether this item was of the same or a different color as the memory item that had previously been presented at that location. In cued trials, the test item was presented at the location of the cued item. All locations were equally likely to be tested, but chosen in a randomized order. The color of the test item was either identical to the color of the memory item that had previously been presented at that location or a different, spectrally neighbouring color. The shape of the test item was always that of the memory item that had previously been presented at the respective location. The test item was present until response, but a quick decision was encouraged. Participants responded by pressing a button with their right index or middle finger, and the response assignment was balanced across participants.

In no-TMS trials, the inter-trial interval (ITI) was one second. For safety reasons, the ITI was increased to ten seconds in TMS blocks. A separate control experiment (see sections 2.5 and 3.1) was conducted to investigate the effects of these different ITI durations.

2.4 Design

The experiment consisted of 864 trials. There were 288 trials for each TMS condition (noTMS, LO, and SMG) with 144 trials for each retrocue type (spatial and shape), half of which were cued and the other half neutral. Retrocue type was varied blockwise and changed every three blocks of 24 trials each. A block design was chosen, because this has previously been shown to yield significant benefits for different types of retrocues (Heuer & Schubö, 2016a; Li & Saiki, 2014), whereas a study using a trial-by-trial change failed to observe benefits for retrocue types that were not directly spatial (Berryhill, Richmond, Shay, & Olson, 2012). The order in which the retrocue types were presented was balanced across participants. Cued and neutral trials were randomly interleaved within these blocks.

Testing took place in four sessions in consecutive weeks. Each session started with three noTMS blocks, followed by six blocks with TMS: in the first two sessions one TMS site was stimulated and in the last two the other TMS site. The order in which the two TMS sites were stimulated was balanced across participants. We did not use separate TMS sites or sham TMS as controls, because the design aimed at a double dissociation: The two sites provided controls for each other and for any non-specific effects of TMS (e.g., the clicking sound of the TMS coil), which would affect either both or none of the stimulation sites. Similar designs have been successfully used in other TMS studies (e.g., Malik, Dessing, & Crawford, 2015; Pelgrims, Andres, & Olivier, 2009; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009). Prior to the first session, every participant completed a short training session on a separate day.

2.5 ITI control experiment

Sixteen volunteers (fourteen females; mean age: 21 years, SD = 3 years; one left-handed) participated in the control experiment. None of them had also participated in the main experiment. Stimuli, task and design were the same as in the main experiment, except for the following. The experiment consisted of 288 trials. For one half of the experiment, the ITI was long (ten seconds, as in the TMS blocks in the main experiment), and for the other half of the experiment, the ITI was short (one second, as in the noTMS blocks in the main experiment). The order of long and short ITIs was balanced across participants. The *d'* scores were calculated separately for long and short ITIs, and for cued and neutral trials.

2.6 Localization of brain sites and TMS protocol

To localize the stimulation sites and monitor the TMS coil position, a frameless stereotaxic neuronavigation system (Brainsight, Rogue Research, Montréal, Canada) was used. Three-dimensional structural T_1-weighted MRIs were obtained for all participants prior to the behavioral sessions. The two stimulation sites in the right hemisphere were identified individually for each participant according to anatomical criteria and based on previous studies (Chambers, Payne, & Mattingley, 2007; Cohen, Cross, Tunik, Grafton, & Culham, 2009; Large, Aldcroft, & Vilis, 2007). SMG was defined as the region adjacent to the dorsolateral projection of the lateral sulcus, posterior to the post-central sulcus and anterior to the superior temporal sulcus (average Talairach coordinates: 49, -33, 37; average MNI coordinates: 54, -31, 39). LO was near the junction of the inferior temporal sulcus and the lateral occipital sulcus (average Talairach coordinates: 37, -70, -2; average MNI coordinates: 40, -73, -1). Figure 1b shows the stimulation sites in the right hemisphere of one participant.

In each trial of the TMS blocks, a repetitive pulse train consisting of three pulses with a frequency of 10 Hz was delivered 100 ms after cue onset. Stimulation intensity was fixed to 60% of the stimulator output. These stimulation parameters were chosen based on previous studies (Chambers et al., 2007; Mullin & Steeves, 2011; Pitcher et al., 2009; Schenkluhn et al., 2008). The delay of 100 ms between retrocue presentation, and the following timing of the three pulses ensured that the stimulation did not affect perceptual processing of the retrocue, but effectively covered the temporal range of its attentional processing (see also Souza & Oberauer, 2016). TMS was administered using a Magstim Rapid 2 system and a 70 mm figure-of-eight coil that was held tangentially to the scalp surface.

2.7 Data analysis

Trials with excessively long reaction times (> 2.5 SD from mean RT calculated individually for each participant) were excluded from further analysis (on average, 3% of all trials). The dependent variable for all analyses was the sensitivity of change detection (*d'*). The *d'* scores were calculated as *d'* = z(hit rate) – z(false alarm rate). For the analysis of the stimulation effects, the *d'* scores in the noTMS condition were used as baseline and subtracted from the *d'* scores in the corresponding TMS conditions. Additionally, mean reaction times were analyzed to ensure that speed-accuracy trade-offs did not contribute to any differences in accuracy as assessed by *d'*. For reaction times, only trials with correct responses were included. Measures were computed separately for the different TMS conditions, retrocue types, and for cued and neutral trials. Neutral trials were identical in all blocks of trials, and only differed in that they were interleaved with different types of cued trials. However, neutral trials were analyzed separately for the different TMS conditions and retrocue types.

3. Results

3.1 ITI control experiment

Figure 2 shows the sensitivity of change detection (*d'*) for short and long ITIs, separately for cued and neutral trials. A two-way repeated measures analysis of variance (ANOVA) with the factors retrocue type (cued vs. neutral) and ITI duration (short vs. long) showed that performance was better in cued than in neutral trials ($F_{(1,15)} = 24.84$, $p < .001$, partial $\eta^2 = .62$) and overall it was also better with long ITIs than with short ITIs ($F_{(1,15)} = 10.72$, $p = .005$, partial $\eta^2 = .42$). An interaction

($F_{(1,15)}$ = 4.83, p = .044, partial η^2 = .24) revealed that the performance with long and short ITIs differed between cued and neutral trials. Follow-up t-tests showed that performance was better in cued than in neutral trials with both short ITIs ($t_{(15)}$ = 5.66, p < .001) as well as long ITIs ($t_{(15)}$ = 2.22, p = .022). Importantly, sensitivity (*d'*) was significantly better with long ITIs than with short ITIs ($t_{(15)}$ = 4.04, p = .001) only in neutral trials, whereas it was equivalent with long and short ITIs in cued trials ($t_{(15)}$ = 1.69, p = .111). Thus, ITI duration improved performance in neutral trials, but not in cued trials. Presumably, the long ITI reduced intertrial interference, which improved performance when memory load was high (i.e., in neutral trials), but not when memory load was already essentially reduced to one item (i.e., in cued trials). Our statistical analyses of the main experiment were consequently designed in such a way that this differential effect of ITI duration did not affect the conclusions. In particular, the analyses testing for region-specific TMS-induced effects were not performed on the retrocueing benefits (*d'* scores in cued trials minus *d'* scores in neutral trials), but separately for cued and neutral trials.

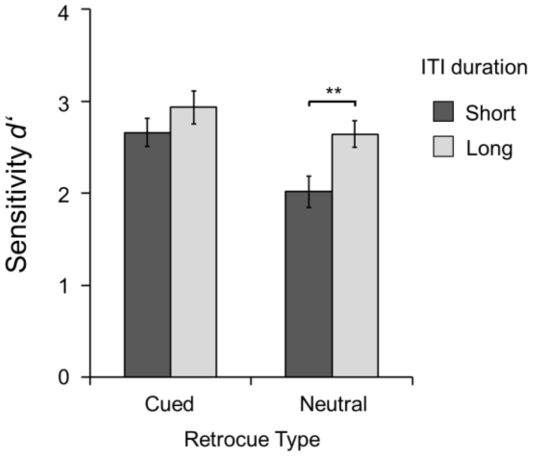

Figure 2. Results of the ITI control experiment. Sensitivity of change detection (*d'*) is shown separately for short (dark grey) and long (light grey) ITI durations, and for cued (left) and neutral (right) trials. Error bars show the standard errors of the means. Asterisks mark significant differences between short and long ITIs (** p < .01).

3.2 Main experiment

Figure 3a shows the sensitivity of change detection (*d'*) for the two retrocue types (spatial vs. neutral) and for each TMS condition (noTMS vs. LO vs. SMG), separately for cued and neutral trials. Three analyses were performed on these data. First, to test whether there was a general improvement in performance in cued compared to neutral trials for both types of cues, a two-way repeated measures ANOVA with the factors retrocue information (cued vs. neutral) and retrocue type (spatial vs. shape) was performed on the *d'* scores in the noTMS condition (see Figure 3a). Indeed, *d'* scores were higher in cued than in neutral trials ($F_{(1,10)} = 25.23$, $p = .001$, partial $\eta^2 = .72$).

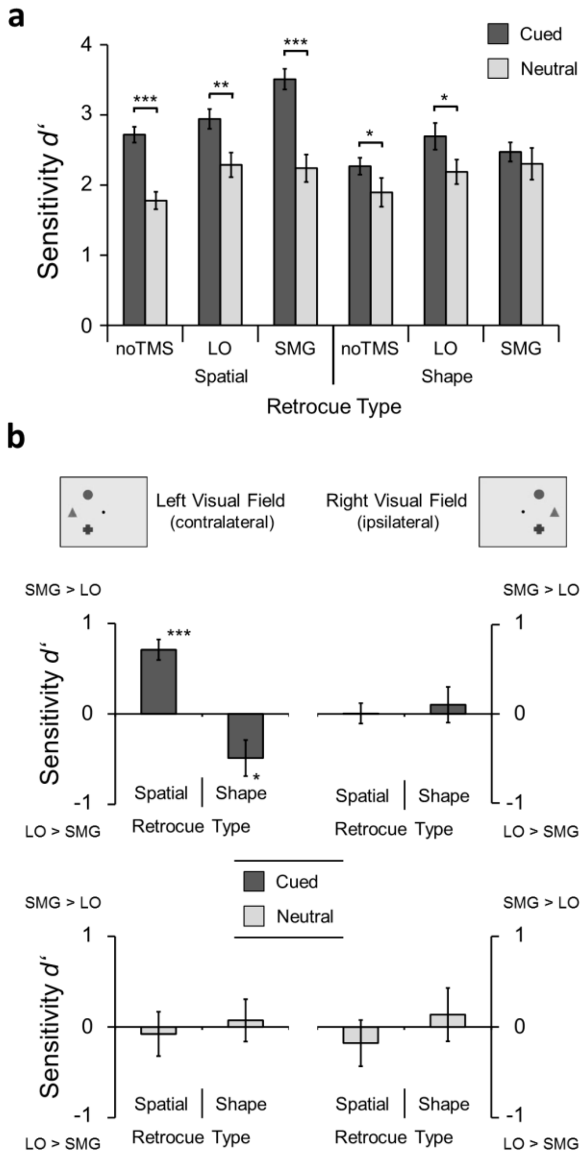

Figure 3. Results of the main experiment. (**a**) Sensitivity of change detection (*d'*) shown for the different retrocue types, averaged across TMS conditions. Asterisks mark significant differences between cued and neutral trials (* p < .05; *** p < .001; one-tailed t-tests). (**b**) Differential effects of the two TMS sites relative to the no-TMS baseline (SMG minus LO), shown separately for left- and right-hemifield trials and for cued (dark grey, upper row) and neutral trials (light grey, bottom row). Positive values indicate improved performance with TMS to SMG, negative values indicate improved performance with TMS to LO. Asterisks mark significant differences from zero (two-tailed t-tests). Error bars show standard errors of the means.

An interaction revealed that this difference was larger for spatial retrocues ($F_{(1,10)} = 8.19$, $p = .017$). Follow-up t-tests (one-tailed) confirmed that there were, as expected, significant benefits in the sensitivity of change detection (*d'*) for both shape ($t_{(10)} = 2.24$, $p = .0245$) as well as spatial retrocues ($t_{(10)} = 5.84$, $p < .001$). The corresponding pattern of results was observed for reaction times. Reaction times were faster in cued than in neutral trials ($F_{(1,10)} = 64.58$, $p < .001$, partial $\eta^2 = .87$), and this difference was larger for spatial retrocues $F_{(1,10)} = 7.39$, $p = .022$, partial $\eta^2 = .43$). T-tests confirmed that there were significant benefits in terms of reaction time for both shape ($t_{(10)} = 7.75$, $p < .001$) and spatial retrocues ($t_{(10)} = 5.13$, $p < .001$). Moreover, reaction times were faster in spatial retrocue blocks than in shape retrocue blocks ($F_{(1,10)} = 23.09$, $p = .001$, partial $\eta^2 = .70$). Thus, participants were able to attentionally select a task-relevant item based on either location or shape, yielding improved memory performance for that item.

Second and third, to test for overall effects of the stimulation, two-way repeated measures ANOVAs with the factors retrocue type (spatial vs. shape) and TMS condition (noTMS vs. LO vs. SMG) were computed separately for cued and neutral trials (see sections 2.5 and 3.1) (see Figure 3a). For neutral trials, there was a significant main effect of TMS condition ($F_{(2,20)} = 4.76$, $p = .02$, partial $\eta^2 = .32$). Subsequent pairwise comparisons revealed a significant difference between noTMS and LO (-.40 ± .13, $p = .041$), and the difference between noTMS and SMG just failed to reach significance (-.43 ± .15, $p = .053$). Performance for trials with stimulation of LO and SMG did not differ (-.03 ± .18, $p = 1$). This overall enhancement in TMS blocks compared to noTMS blocks in neutral trials might be due to the longer ITI duration, and not an effect of the stimulation per se (see section 3.1). There was neither a significant main effect of retrocue type nor an interaction for neutral trials. For cued trials, performance was better with spatial retrocues than with shape retrocues, as shown by a main effect of retrocue type ($F_{(1,10)} = 55.19$, $p < .001$, partial $\eta^2 = .85$). There was also a main effect of TMS condition, with significant differences between noTMS and LO (-.33 ± .08, $p = .006$) and between noTMS and SMG (-.50 ± .10, $p = .001$), but not between LO and SMG (-.17 ± .11, $p = .55$). Our main interest, however, was in investigating differential TMS-induced effects on attentional selection based on location vs. shape. Indeed, a significant interaction ($F_{(2,20)} = 6.08$, $p = .009$, partial $\eta^2 = .38$) revealed that the effects of TMS condition differed between retrocue types and more specific analyses were performed to further elucidate this interaction (see below). The same ANOVAs were computed for reaction times. For both cued as well as neutral trials, there were only significant main effects of retrocue type (*cued* $F_{(1,10)} = 11.58$, $p = .007$, partial $\eta^2 = .54$; *neutral* $F_{(1,10)} = 5.87$, $p = .036$, partial $\eta^2 = .37$) and neither significant effects of TMS condition nor interactions. Thus, there was no speed-accuracy trade-off, and TMS did not affect reaction times.

In order to specifically test for region-specific differential TMS-induced effects while simultaneously controlling for non-specific TMS effects, we subtracted the *d'* values in LO trials from the values in SMG trials after no-TMS baseline correction. This was done separately for the different retrocue types and for the left- and right-hemifield trials (Figure 3b). Note that positive values indicate a greater improvement in performance for TMS over SMG, whereas negative values indicate a greater improvement in performance for TMS over LO. Two-way repeated measures ANOVAs with the factors retrocue type (spatial vs. shape) and visual field (left vs. right) were computed separately for cued trials (Figure 3b, upper row) and for neutral trials (Figure 3b, bottom row). For cued trials, a significant main effect of retrocue type ($F_{(1,10)} = 10.45$, $p = .009$, partial $\eta^2 = .51$) confirmed that values were higher (and positive) for spatial retrocues, and lower (and negative) for shape retrocues. Moreover, there was a significant interaction of retrocue type and visual field ($F_{(1,10)} = 20.75$, $p = .001$, partial $\eta^2 = .68$), and follow-up t-tests against zero revealed that the site-differentiated enhancement was only observed for the left visual field (contralateral to TMS sites): a positive value for spatial retrocues ($t_{(10)} = 6.23$, $p < .001$) indicated relatively enhanced performance with TMS to SMG, and a negative value for shape retrocues ($t_{(10)} = 2.45$, $p = .034$) indicated relatively enhanced performance with TMS to LO. No effects were observed for neutral trials.

4. Discussion

Our results show that spatial and feature-based attentional selection of VWM representations recruit distinct cortical regions: Stimulation of SMG selectively facilitated spatial attention, whereas stimulation of LO selectively facilitated feature-based attention. This demonstrates, for the first time, that there are specialized cortical modules for the selection of memory contents based on different visual properties.

This cortical dissociation indicates that the basic differentiation between feature-based and spatial attention that has long been established for the perceptual domain also applies to the mnenomic domain. Specifically, SMG and LO have previously been implicated in attentional orienting based on object location and shape in the external world (Chambers et al. 2004; Murray & Wojciulik, 2004; Schenkluhn et al., 2008), which suggests that spatial and feature-based attentional mechanisms utilize similar neural machinery when operating on perceptual input and on mnemonic representations.

From a broader perspective, the idea of overlapping perceptual and VWM attentional systems is consistent with reports of highly overlapping activations for orienting attention in perception and in VWM, involving a large network of frontal, parietal and occipital areas (Lepsien & Nobre, 2006). Our results reveal a specialization of certain brain areas within the neural network involved in attentional selection in VWM with respect to the type of attended stimulus characteristic. This finding can also be seen as in line with what has been shown for the perceptual domain. Studies typically report the activation of a largely overlapping network, indicating a common control system, with subregions or populations of neurons within this network that are preferential or specific for controlling either spatial or feature-based attention (Giesbrecht, Woldorff, Song, & Mangun, 2003; Slagter et al., 2007; Vandenberghe, Gitelman, Parrish, & Mesulam, 2001). In light of the correspondence between our results and findings on perceptual attention, it would be a parsimonious hypothesis that the neural implementation of spatial and feature-based attentional selection involves overlapping substrates, specifically SMG and LO.

This need not imply that selective attention for visual perception and VWM share identical circuitry. The brain must also be able to differentiate perceptual input from memory, and be able to selectively deploy attention in these two domains. This selective gating might occur at the level of the microcircuitry and output connections of SMG and LO, as well as in the executive control mechanisms that deploy and gate these modules. An obvious candidate for this function might be prefrontal cortex (e.g., Gazzaley & Nobre, 2012; Kuo, Stokes, Murray, & Nobre, 2014; Lee & D'Esposito, 2012; Zanto, Rubens, Thangavel, & Gazzaley, 2011). Interestingly, differences in the neural substrates of attentional selection in perception and VWM have mostly been observed in frontal areas, with increased frontal involvement for orienting attention in VWM (Nobre et al, 2004; Tanoue, Jones, Peterson, & Berryhill, 2013). Thus, attention for perception and attention for VWM might share circuitry, while the brain also retains the ability to deploy these forms of attention differentially.

The double dissociation between SMG and LO on attentional orienting based on location and shape was only observed for the visual hemifield that was contralateral to the stimulation sites. This lateralization may be due to the nature of the representations that attention operates on when selecting information in VWM, for which hemispheric lateralization has previously been demonstrated (e.g., Gratton, 1998; Vogel & Machizawa, 2004). While such lateralization is common to the visual system, to our knowledge this is the first time a lateralized effect of TMS on directing attention in VWM has been demonstrated. This finding is consistent with electrophysiological studies reporting lateralized event-related and oscillatory activity following the presentation of retrocues, that is, for selecting representations in VWM (Griffin & Nobre, 2003; Myers et al., 2015; Poch et al., 2014).

Our finding of a TMS-induced enhancement of cognitive performance was rather surprising given that previous studies using a similar protocol and / or stimulating SMG or LO have mostly observed an impairment of performance (e.g., Bona, Herbert, Toneatto, Silvanto, & Cattaneo, 2014; Chambers et al., 2004; Mullin & Steeves, 2011; Romei, Gross, & Thut, 2010; Schenkluhn et al, 2008). The mechanisms of TMS are poorly understood, and whether it results in facilitatory or disruptive effects may depend on a number of stimulation parameters (Luber & Lisanby, 2014). Our triple-pulse rTMS may have modulated oscillatory brain activity in the alpha band. Particularly rTMS delivered at individual alpha frequency, which on average is 10Hz and thus equal to our stimulation frequency, has been associated with facilitatory effects on cognitive performance (Klimesch, Sauseng, & Gerloff, 2003; Luber & Lisanby, 2014). Modulating alpha power using anodal transcranial direct current stimulation has been found to improve performance in a change detection task that involved visual working memory, presumably due to a change in the attentional state (Hsu, Tseng, Liang, Cheng, & Juan, 2014). Alpha-band oscillations have recently also been specifically implicated in the attentional selection of VWM representations (Myers et al. (2015). In light of evidence linking alpha-band oscillations to inhibitory mechanisms (Klimesch, 2012; Sauseng et al., 2009), it could be that the facilitation of attentional selection was not mediated by an enhancement of the selected representation (i.e., the cued item) but by facilitated inhibition of the nonselected representations (i.e., the uncued items) (see also Tseng et al., 2012).

Regardless of the mechanism, the TMS-induced performance enhancement that we observed could be valuable for the development of TMS-based neurorehabiliation therapies for VWM deficits. TMS-based rehabilitation therapies are still in the early stages of development, but there have been a number of successful uses (Luber & Lisanby, 2014). Establishing the association between a particular TMS protocol and enhancement of a specific cognitive function is an important first step.

When interpreting these findings, we considered several concerns that are not directly related to the TMS-induced effects. For one, one might argue that a verbal strategy was adopted, and that participants accordingly memorized the names of the colors. However, several previous studies similarly used categorical colors as the feature to be memorized, and concluded that performance in such tasks relies on visual working memory (e.g., Heuer & Schubö, 2016b; Ikkai, McCollough, & Vogel, 2010; Kuo, Stokes, & Nobre, 2012), rather than verbal working memory (e.g., Luck & Vogel, 1997; Luria, Sessa, Gotler, Jolicoeur, & Dell'Acqua, 2010). Further, it seems more likely that TMS over LO and SMG (which are well-known 'highlevel' visual areas) would have affected visual working memory than a verbal strategy.

Second, the retrocueing benefits in the noTMS condition were considerably smaller for shape retrocues than for spatial retrocues. A potential explanation for this observation is that some participants memorized color-location bindings and ignored shape information. However, out of the eleven participants, only three did not show a benefit with shape retrocues in the noTMS condition, and only one participant did not show a benefit with stimulation of LO. Thus, shape information was clearly available to make use of the shape retrocue, and there was no indication that participants adopted the strategy of ignoring shape information altogether. There is evidence indicating that even task-irrelevant features of objects are automatically encoded, with only subsequent maintenance being under voluntary control (Marshall & Bays, 2012; Xu, 2010). Given that shape was required to make use of the retrocue, it seems reasonable to assume that this feature was encoded and maintained along with color and location in an object-based manner (see also Luck & Vogel, 1997; Luria & Vogel, 2011). In support of this, two recent studies showed that tasks that emphasize feature binding (which was the case here) encourage the storage of integrated objects (Balaban & Luria, 2016; Vergauwe & Cowan, 2015). In a previous study using a very similar design (Heuer &

Schubö, 2016), we observed equivalent overall benefits for shape and spatial retrocues. We did not systematically analyze individual differences in that study, but it does seem that some people preferred one type of retrocue over the other, yielding larger benefits for this preferred cue type.

To conclude, we have shown that different cortical areas subserve spatial and feature-based selection of VWM representations, indicating that these are distinct attentional mechanisms. The correspondence between our findings and what has been established for perceptual attention suggests that these types of top-down control over mnemonic representations and perceptual input are similarly implemented in parietal and occipital cortex. In general, these results provide novel insight into how attentional mechanisms operating on different kinds of information optimize the visual system, allowing for an efficient use of the limited VWM system.

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Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author contributions

AH, AS and JC designed research, AH collected and analyzed data, AH, AS and JC wrote the paper.

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Study IV

Action-relevance induces an attentional weighting of representations in visual working memory

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Abstract

Information maintained in visual working memory can be strategically weighted according to its task-relevance. This is typically studied by presenting cues during the maintenance interval, but under natural conditions, the importance of certain aspects of our visual environment is mostly determined by intended actions. Here, we investigated whether representations in visual working memory are also weighted with respect to their potential action-relevance. In a combined memory and movement task, participants memorized a number of items and performed a pointing movement during the maintenance interval. The test item in the memory task was subsequently presented either at the movement goal or at another location. We found that performance was better for test items presented at a location that corresponded to the movement goal than for test items presented at action-irrelevant locations. This effect was sensitive to the number of maintained items, suggesting that preferential maintenance of action-relevant information becomes particularly important when the demand on visual working memory is high. We argue that the weighting according to action-relevance is mediated by the deployment of spatial attention to action goals, with representations spatially corresponding to the action goal benefitting from this attentional engagement. Performance was also better at locations next to the action goal than at locations farther away, indicating an attentional gradient spreading out from the action goal. We conclude that our actions continue to influence visual processing at the mnemonic level, ensuring the preferential maintenance of information that is relevant for current behavioural goals.

Introduction

The way we perceive the visual world around us is strongly influenced by what we are doing or intending to do. From the vast amount of information available at every moment, the visual system filters out what is relevant for our current behavioural goals, and may thus be seen as a system optimized for gathering action-relevant visual information about our environment. This action-related selective processing of visual information is often referred to as "selection-for-action" (Allport, 1987). The assumption of a close relationship between visual perception and action has received substantial empirical support (e.g., Schütz-Bosbach & Prinz, 2007), but selective processing continues to be essential for the visual system beyond the perceptual stage, namely for maintaining relevant visual information over short periods of time. In the present experiments, we investigated whether selection for action also occurs during maintenance in visual working memory (VWM).

Action planning and visual attention

Early evidence for a coupling of action planning and visual selection was provided by studies in which participants were to perform saccadic eye movements in combination with a visual detection, discrimination or identification task. Hoffman and Subramaniam (1995) had participants saccade to one of four locations and detect a target letter briefly presented at one of the locations before the movement was initiated. Detection accuracy was best when the target letter had been presented at the saccade goal, even when participants were explicitly cued to attend to another location. Similar results were obtained by Kowler, Anderson, Dosher, and Blaser (1995) who combined an eye movement with a letter identification task. This obligatory coupling between saccade programming and visual attention appears to be spatially specific to the intended location rather than to the actual landing position of the saccade (Deubel & Schneider, 1996). When sequences of saccadic eye movements were to be executed, performance in an identification task was better at any of the saccade goal locations than at any of the other locations, suggesting that attention was allocated in parallel to all movement goals (Baldauf & Deubel, 2008a; Godijn & Theeuwes, 2003).

One could assume that movements of the eyes are special in that the link between overt and covert attention is particularly strong (see also Rizzolatti, Riggio, Dascola & Umiltá, 1987), but remarkably similar conclusions have been drawn for hand movements (for a review, see Baldauf & Deubel, 2010). In several studies, Deubel and colleagues have shown that during the preparation of manual pointing movements, performance in a visual task was best at the location of the pointing goal, indicating that attention was shifted to the goal location prior to movement onset (Baldauf & Deubel, 2008b, 2009; Baldauf, Wolf, & Deubel, 2006; Deubel, Schneider, & Paprotta, 1998). This coupling of attention to the movement goal location was observed in spite of participants' knowledge of the location of the visual target (Deubel et al., 1998), suggesting that it is obligatory. In addition to these studies on how spatial attention is linked to an action goal, others have demonstrated the impact of manual actions on the attentional weighting of features (e.g., Craighero, Fadiga, Giacomo, & Umiltà, 1999; Müsseler & Hommel, 1997) and feature-dimensions (e.g., Fagioli, Hommel, & Schubotz, 2007; Wykowska, Schubö, & Hommel, 2009) in visual search or visual discrimination tasks.

Presumably, the deployment of spatial attention to a movement goal serves to ensure that all the relevant information necessary to specify movement parameters is available and preferentially processed. Given that processing efficiency has been shown to decrease when attention is distributed over a larger region of the visual field (e.g., Castiello & Umilta, 1990; Müller, Bartelt, Donner, Villringer & Brandt, 2003), attentional deployment should ideally be spatially specific to the actual movement goal. Indeed, a high spatial specificity has been demonstrated for manual pointing movements (Baldauf et al., 2006; Deubel et al., 1998). When there are multiple pointing movement goals, such as for bimanual movements and movement sequences, attention appears not to be uniformly distributed across the visual field. Rather, movement-relevant goal locations are selected in parallel by spatially distinct attentional foci, whereas intermediate locations remain unattended (Baldauf & Deubel, 2008b, 2009; Baldauf et al., 2006).

Interestingly, the intention to perform a movement does not seem to be necessary to affect visual perception, but the mere presence of a hand near visual stimuli alters their processing. Reed, Grubb, and Steele (2006) had participants place one hand next to one of the target locations in a covert attention task, and observed facilitated detection of targets near the hand. The authors proposed that this nearby-hand effect might be due to an attentional prioritization of space near the hand. Other studies have corroborated this idea. Using three classic attention paradigms (visual search, inhibition of return, and attentional blink), Abrams, Davoli, Du, Knapp, and Paull (2008) were able to show that a nearby hand disrupted attentional disengagement, indicating a more detailed evaluation of objects in the perihand space. An extended analysis of objects that are near the hand can be assumed to optimize potentially upcoming actions by providing the relevant visual information. Indeed, visual sensitivity in the perihand space has been shown to be improved (Dufour & Touzalin, 2008). Moreover, a recent neurophysiological study provides evidence of a modulation of neuronal responses in an early visual area, namely a sharpening of orientation tuning and reduced response variability of neurons in macaque area V2 in the presence of a nearby hand (Perry, Sergio, Crawford, & Fallah, 2015).

Attentional modulation of maintenance in VWM

VWM as that part of the visual system that allows us to maintain and manipulate visual information over short periods of time is important for higher cognitive functions and even simple actions such as saccades. Because the capacity of VWM is highly limited (Cowan, 2001; Fukuda, Awh, & Vogel, 2010; Luck & Vogel, 1997), selective processing is crucial for its optimal use, necessitating attentional mechanisms not only for selecting the most relevant information for encoding, but also for updating and weighting VWM contents. Indeed, attentional mechanisms modulate VWM throughout all processing stages, from encoding to retrieval (Gazzaley & Nobre, 2012). During maintenance, attention can be directed towards specific representations, improving memory for the respective selected information (e.g., Astle, Summerfield, Griffin, & Nobre, 2012; Griffin & Nobre, 2003; Nobre et al., 2004). Irrelevant information can be excluded from memory (Kuo, Stokes, & Nobre, 2012; Williams, Hong, Kang, Carlisle, & Woodman, 2013), or a weighting of information according to its relevance can be introduced by means of maintenance in different representational states, within and outside an internal focus of attention (e.g., Heuer & Schubö, submitted; LaRocque, Lewis-Peacock, & Postle, 2014; Rerko & Oberauer, 2013; Zokaei, Ning, Manohar, Feredoes, & Husain, 2014). Moreover, representations can be flexibly selected based on whatever type of stimulus characteristic determines their relevance, be it their spatial location or a feature (Heuer & Schubö, 2016; Li & Saiki, 2014; Pertzov, Bays, Joseph, & Husain, 2013).

Experimentally, the attentional selection of relevant representations is typically induced by presenting a so-called retrocue during the retention interval, indicating certain items as more behaviourally relevant than others. Most studies used spatial retrocues that indicated one or several item(s) by pointing towards the location(s) at which the item(s) had previously been presented. Outside the laboratory, however, the relevance of certain aspects of our visual environment is not specified by an external event, but mostly (if not always) determined by what we are intending to do. Thus, it seems reasonable to assume that our actions do not only influence which visual information we prioritize in perception, but also which visual information we maintain. One study reported improved performance with nearby hands in a change detection task, which requires the use of VWM (Tseng & Bridgeman, 2011). However, in these experiments, the hands were continuously placed at the monitor during the trials, so that, as the authors themselves suggest, the observed improvement could be the result of perceptual facilitation and not an improvement of working memory per se. To our knowledge, the idea that intended action might influence attention in VWM has not been directly tested.

Rationale of the experiments

In two experiments, we investigated whether the contents of VWM are weighted according to their potential action relevance. As outlined above, spatial attention is automatically drawn to the location of an action goal, and the deployment of spatial attention to items in VWM improves memory for these items. Thus, we hypothesized that performing a movement towards a specific location would result in the allocation of spatial attention to that location, and that memory items that had previously been presented at that location would benefit from this attentional bias, yielding improved memory for these items. In a dual-task paradigm, participants had to memorize a number of objects and perform a pointing movement during the retention interval. The location of the item subsequently tested in the memory task either corresponded to the movement goal location, or it was presented at an action-irrelevant location.

In contrast to studies that used retrocues to manipulate task-relevance, all memory items were equally relevant for the memory task, but only differed in their *potential action-relevance*. We expected better performance for items that had been presented at movement goal locations than for items that had been presented at action-irrelevant locations. As selective processing is particularly important for the capacity-limited VWM, we additionally investigated whether action-related selective processing would receive priority when VWM reaches its capacity, that is, when memory load is increased to its limit (Experiment 1), and the spatial specificity of the effect relative to the movement goal (Experiment 2). Control conditions without a movement (Experiment 1) and with a movement to a goal that never corresponded to the test item location in the memory task (Experiment 2) served to ensure that any observed effects were not due to perceptual priming resulting from the movement cue or general, spatially unspecific action planning processes.

Experiment 1

Experiment 1 tested whether representations in visual working memory are weighted with respect to their potential action-relevance. In a dual-task paradigm, participants memorized the orientation of a varying number of memory items The memory items were presented among task-irrelevant distractor items, which were included so that the number of memory items could be varied while keeping the total number of items constant. During the retention interval, a cue indicated the movement goal. In movement blocks, participants were then to execute a pointing movement towards that location. In control blocks without movement, participants were instructed not to respond to the cue. The subsequent test item in the memory task was either presented at a location corresponding to the cued location, or at a location that did not correspond to the cued location.

Several potential outcomes may be expected. First, the cue may have no effect on memory performance, given that it is entirely irrelevant to the memory task. If so, memory performance should be similar for all items independent of whether their location corresponded to the cued location. Second, as spatial cues such as arrows are known to guide attention at least to some extent (Hommel, Pratt, Colzato, & Godijn, 2001; Ranzini, Dehaene, Piazza, & Hubbard, 2009), the cue may cause participants to deploy their attention to the location indicated by the cue. This would result in cueing benefits, namely better memory performance for items presented at locations corresponding to the cued location compared to items at non-corresponding locations. Finally, if action planning causes a specific attention bias, that is, a weighting of representations in VWM due to an attentional bias at movement goal locations, such cueing benefits should be even more pronounced in movement blocks than in control blocks without movement execution (pointing benefits).

Methods

Participants

Thirty students of Philipps-University Marburg participated in the experiment. Data from two participants had to be excluded due to poor performance in the memory task (< 50%). The remaining participants (21 female, 7 male, mean age = 22 years) were right-handed and had normal or corrected-to-normal visual acuity and normal colour vision. Visual acuity and colour vision were tested with the OCULUS Binoptometer 3 (OCULUS Optikgeräte GmbH, Wetzlar, Germany). All participants provided informed written consent and were naive to the purpose of the experiment.

Apparatus

Participants were seated in a comfortable chair in a dimly lit room, facing a monitor at a distance of approximately 104 cm from their eyes. In front of the monitor, placed at a distance of approximately 55 cm from the participants' eyes, a framed glass plate was mounted on a table. Pointing movements were performed towards this glass plate. For each participant, the glass plate was adjusted in height to ensure that it covered the entire monitor. Participants had a wooden board in front of them with a response box to the left, and a movement pad to the right. To respond to the memory task, participants pressed the two buttons on the response box using their left middle and index fingers. The right hand was positioned on the movement pad with a cross to mark the starting position for index finger and thumb. Stimuli were presented on a 22" screen (1680 x 1050 px). Stimulus presentation and response collection were controlled by a Windows PC using E-Prime 2.0 software (Psychology Software Tools, Inc.).

Pointing movements were recorded using a Polhemus Liberty 240/8 (Polhemus Inc) magnetic motion tracking device measuring x, y and z coordinates at a sampling rate of 240 Hz. Its source was placed 70 cm in front of the participant, under the table upon which the glass plate was mounted. A sensor was fixed on top of the tip of participants' right index finger. Movement data collection was controlled using MATLAB.

Task and stimuli

The task is illustrated in Figure 1. A trial started with the presentation of a memory array consisting of differently oriented bars for 200 ms. The number of memory items (set size) was varied between one and five. Colour (red/blue) served to distinguish memory and distractor items.

For instance, memory items were presented in blue and distractor items in red (see Figure 1). The colour assignment that defined memory and distractor items was balanced across participants. Participants were instructed to memorize the orientations of the memory items, and ignore the other items. After 800 ms, the memory array was followed by the presentation of a spatial cue for 200 ms. This cue pointed to one of the eight locations of the items, which were marked by circle outlines throughout the experiment. The cued location could be the previous location of a distractor item, of the memory item that would subsequently be tested in that trial, or of another memory item. Participants were to point towards this location by touching the glass plate between them and the monitor with the tip of their right index finger. Participants then moved their hand back to the start position in front of them, where it remained during the experimental trials. In control blocks without movement execution, participants were instructed to ignore the cue. After another interval of 800 ms after the end of the movement (or after 1500 ms in control blocks), a test item was presented at one of the locations of the memory items, and participants were to indicate whether this test item was of the same or of a different orientation as the memory item that had previously been presented at that location. The response assignment was balanced across participants. The test item was present until response, but participants were encouraged to respond quickly.

All stimuli were presented against a grey background. The orientation of each memory item was randomly selected from a set of six orientations (15°, 45°, 75°, 105°, 135° and 165°), with the restriction that no two memory items could have the same orientation. The orientations of the distractors were randomly chosen from the same set but without any restrictions, so that multiple distractors could have the same orientation. The orientation of the test item was either identical to that of the respective memory item or randomly selected from the remaining five orientations. Memory and distractor items were blue and red, the test item was always grey. All item colours were isoluminant.

There were eight fixed locations which served as item locations in the memory task and as goals in the pointing task. These locations were arranged on an imaginary circle with a radius of approximately 5.07° of visual angle. Circle outlines (diameter 1.6° of visual angle) marked these locations and were present throughout the entire experiment. The memory, distractor and test items were 0.28° x 1.49° of visual angle in size. The distance between memory items (centre to centre) was 3.53° of visual angle. The movement cue was a line (0.07° x 0.44° of visual angle) originating from the fixation dot. The fixation dot subtended 0.17° of visual angle.

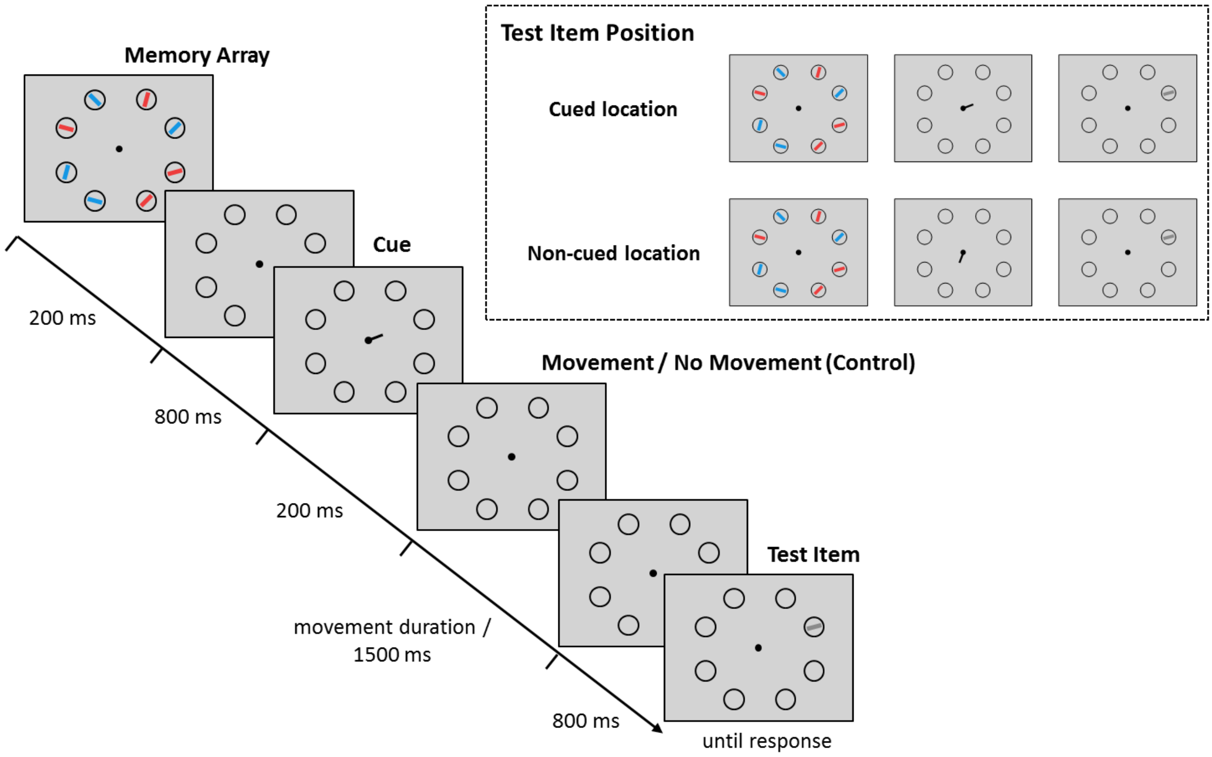

Figure 1. Trial procedure of Experiment 1. A trial started with the presentation of a memory array for 200 ms. Colour indicated the memory items (here in blue). Participants were to memorize the orientation of the memory items. After an interval of 800 ms, a cue was presented for 200 ms that pointed to one of the eight locations. In movement blocks, participants were then to perform a pointing movement to the cued location. In control blocks, participants were instructed not to perform a movement, but to ignore the cue. After completion of the pointing movement in movement blocks, or after a fixed interval of 1500 ms in control blocks, and after another 800 ms, a test item was presented at one of the previous memory item locations. Participants were then to indicate whether this test item was of the same orientation as the memory item that had previously been presented at that location. The box shows examples of trials in which the test item was presented at the cued or at a non-cued location.

Design

Testing took place in two sessions on consecutive days. On the first day, participants performed short training versions of the memory task and of the combined memory and movement task. These data were not entered into the analyses. On the second day, participants performed the main experiment. Afterwards, they filled in a questionnaire to assess strategies and other factors that might affect performance.

The main experiment consisted of 560 trials, organized in blocks of 35 trials each. Set size in the memory task (1, 2, 3, 4 or 5 memory items) and cued location (tested memory item, another memory item, and a distractor item; equally likely) were varied trialwise. Half of all trials were movement trials, in which participants were to execute a pointing movement towards the cued location. The other half were control trials, in which participants were instructed to ignore the cue and not to execute a movement. This was varied blockwise, with a change every two blocks. The order of movement blocks and control blocks was balanced across participants.

Analysis of movement performance

Positional data were used to determine the endpoints of the pointing movements on the glass plate. Trials in which participants failed to execute a movement, and trials with pointing errors or outliers were excluded from further analysis (on average, 2.5% of all movement trials). Trials with pointing errors or outliers were determined separately for each participant and pointing goal. They were defined as trials in which the movement endpoint deviated by more than 2.5 standard deviations from the mean of all movement endpoints on the horizontal or vertical axis.

To control that participants sufficiently differentiated between the eight possible goal locations, we calculated an Index of Location Differentiation. This was the ratio of the mean Euclidean distance between the mean movement endpoints for neighbouring goal locations (“distance between locations”) and the mean Euclidean distance between each movement endpoint and the mean movement endpoint calculated separately for each goal location and then averaged (“distance within locations”). This index becomes larger the more the endpoints of the pointing movements cluster for each goal and differ for different goal locations.

Analysis of memory performance

Trials with excessively long reaction times (> 2.5 SD from mean RT calculated separately for each participant; on average, 2.9% of all trials), pointing errors or pointing outliers were excluded from further analysis. Accuracy in percent and mean reaction time were calculated separately for each set size, for trials with and without a movement, and for trials in which the test item position corresponded to the cued location (corresponding trials) and for trials in which the test item was presented at a non-cued location (noncorresponding trials). Trials in which the cued location was the location of a distractor item were not entered into the analyses, because we were interested in a weighting of items *within* VWM. For reaction times, only correct responses were included.

To calculate cueing benefits, the means for noncorresponding trials were subtracted from the means for corresponding trials, separately for each set size and for movement and control trials. To isolate the benefits resulting from pointing movements, the cueing benefits in control trials were then subtracted from cueing benefits in movement trials, separately for each set size. These pointing benefits indicate the enhanced weighting of maintained items induced by the pointing movement as compared with a potential benefit of the cue itself. A three-way ANOVA with the factors movement (movement vs. no movement), set size and test item position (cued location vs. non-cued location) was computed. In addition, one-tailed t-tests were computed separately for each set size to compare cueing and pointing benefits against zero.

Results and Discussion

The mean Index of Location Differentiation was 5.63 (SD: 1.63) with a range from 1.69 to 9.24. Thus, as illustrated for an example participant in Figure 2A, the endpoints of the movements were well-clustered according to the different target locations: On average, the distance between endpoint clusters was almost 6 times the distance of endpoints within each cluster from their respective mean.

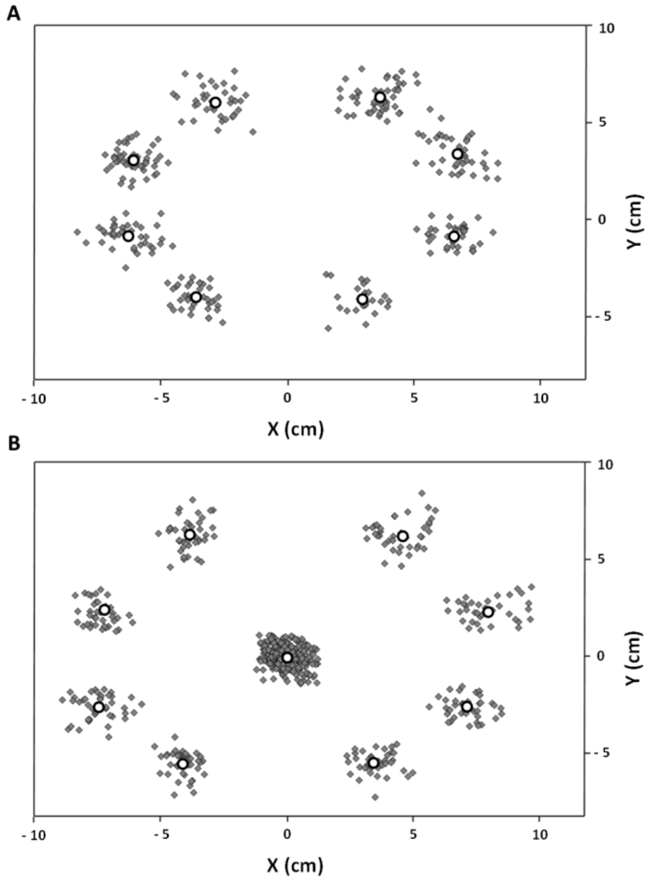

Figure 2. Pointing movement endpoints of a single participant in movement trials in Experiment 1 (A) and in Experiment 2 (B). Circles show the mean endpoints of the different movement goals.

The ANOVA revealed significant main effects of movement (accuracy: $F_{(1,27)} = 28.83$, $p < .001$; reaction time: $F_{(1,27)} = 4.74$, $p = .038$), set size (accuracy: $F_{(3,81)} = 54.26$, $p < .001$; reaction time: $F_{(3,81)} = 9.08$, $p < .001$) and test item position (accuracy: $F_{(1,27)} = 8.4$, $p = .007$; reaction time: $F_{(1,27)} = 6.13$, $p = .02$). Performance in the memory task was better in control trials without a movement, at lower set sizes and at the cued location. Cueing and pointing benefits are visualized in Figure 3A and 3B. Figure 3A shows that performance was improved for test items presented at cued locations (solid lines) as compared to test items presented at non-cued locations (dashed lines). Significant cueing benefits in movement trials were observed for set size three in terms of accuracy ($t_{(27)}$ = 1.86, p = .037) and for set size four in terms of both accuracy ($t_{(27)}$ = 2.9, p = .004) and reaction time ($t_{(27)}$ = 2.5, p = .01). In control trials, there were cueing benefits for set size three (accuracy: $t_{(27)}$ = 1.76, p = .045; reaction time: $t_{(27)}$ = 1.88, p = .036) and for set size five (accuracy: t(27) = 1.88, p = .036). The cueing benefits in the control trials indicate that the presentation of the cue itself influenced performance, even when it was task-irrelevant. Figure 3B shows the pointing benefits, that is, the cueing benefits in movement blocks relative to the cueing benefits in control blocks. Note that positive values for accuracy and negative values for reaction time indicate greater cueing benefits in movement trials as compared to control trials. Pointing benefits, indicating greater cueing benefits in movement trials as compared to control trials, were only observed for a set size of four items, both in terms of higher accuracy ($t_{(27)}$ = 2.59, p = .008) and in terms of shorter reaction times ($t_{(27)}$ = -2.06, p = .03), but not for smaller set sizes of two and three or for a set size of five (Figure 3B).

Given that for the memory task all items were equally task-relevant, it seems plausible that a weighting of information according to potential action-relevance would mainly take effect when the demand on the system is high, that is, when it is likely that not all items can be maintained. Indeed, a set size of four items corresponds to the mean capacity limit of VWM of about four representations (Cowan, 2001; Luck & Vogel, 1997; Zhang & Luck, 2008). Thus, our finding that action intention had the greatest effect for four items suggests that a preferential maintenance of information that may be important for action control because of a spatial correspondence with an action goal becomes behaviourally evident under high load conditions. In analogy to selective visual processing at the perceptual level, this would then be a sort of "selection-for-action" at the mnemonic level in VWM.

At first glance, it might seem surprising that the action intention advantage disappeared for five items. However, there may be a straightforward reason for the reduction of the pointing benefit, though not necessarily for its (statistical) disappearance. Weighting by potential action relevance can only produce a benefit when the item at the movement goal is maintained at the moment the action is planned or executed. With a set size of four this is likely the case in almost all trials, but with a set size of five there is a non-negligible proportion of trials (perhaps more than 20%, assuming that at presentation of the memory set almost 4 of the 5 presented items are selected randomly for maintenance), in which a stronger weighting of the relevant representation would not be possible because that representation is not available. Thus, the statistical significance of the effect would be expected to dissipate for set sizes that exceeded the limits of VWM.

The control condition without movement execution was designed to control for automatic shifts of attention not related to action planning but triggered by the cue itself. Although we

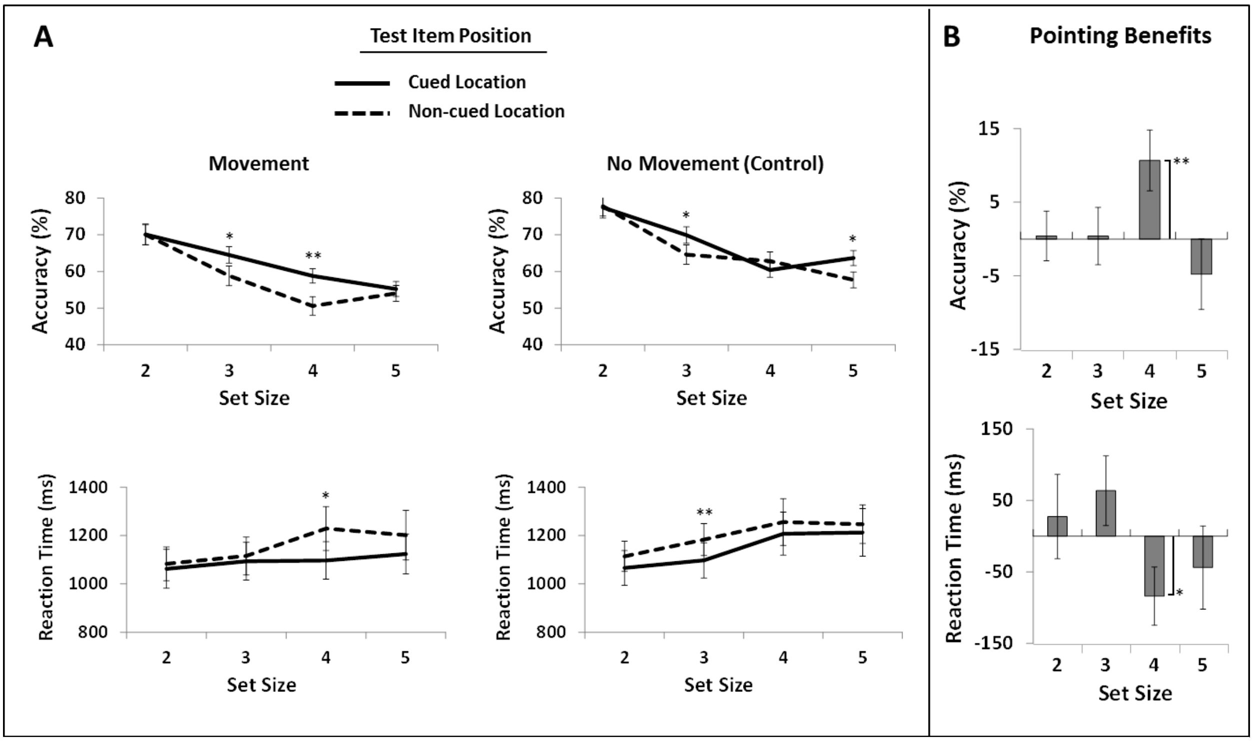

Figure 3. Results of Experiment 1. (A) Accuracy (top) and reaction time (bottom) shown separately for movement (left) and control trials (right), and for the different memory item set sizes. The solid lines show performance for test items presented at the cued location, and the dashed lines show performance for test items presented at non-cued memory item locations. Cueing benefits are the differences in performance for test items presented at cued and at non-cued locations. (B) Pointing benefits (cueing benefits in movement trials minus cueing benefits in control trials) in accuracy (top) and reaction time (bottom). Asterisks mark significant differences from zero (one-tailed t-tests; * $p < .05$; ** $p < .01$). Error bars show standard errors of the means.

instructed participants to ignore the cue in control trials, it is possible that they continued to use the information it contained, as cues presented during the retention interval of a VWM task appear not to be under full strategic control (Berryhill, Richmond, Shay, & Olson, 2012). Centrally presented cues can be considered endogenous cues, that is, they symbolically indicate a location, and automatic attraction of attention has traditionally mainly been associated with exogenous cues abruptly appearing at the stimulus location. However, it has been shown that endogenous cues can trigger automatic shifts of attention as well, if they are sufficiently (over-)learned symbols such as arrows (e.g., Hommel, Pratt, Colzato, & Godijn, 2001; Ranzini, Dehaene, Piazza, & Hubbard, 2009). A line originating from fixation may not be a symbol as overlearned as an arrow, but reflexive shifts of attention have also been observed when associations between a nonpredictive cue and space were arbitrarily chosen and newly learned (Dodd & Wilson, 2009). As control blocks were interleaved with movement blocks in our experiment, it is likely that a strong association between these cues and a spatial location was established. Consistent with this, we observed a slightly improved performance at cued locations in control blocks in the present experiment (see Figure 3A). This may have dampened the relative advantage of intended action in experimental trials, but we still observed it for four items.

Since we did not have a motor task in the control trials, one might argue that the experimental effect was not specific to the influence of intended pointing towards a cued item, but due to a general task-related enhancement. This possibility seems unlikely, because overall performance was higher in the control condition (Figure 3A), suggesting that action planning interfered with performance for non-cued items. However, this concern motivated a second experiment designed to test the spatial specificity of the influence of action planning relative to both a directional cue and the location of the memory item: in the control condition of Experiment 2, participants had to point to a fixed position irrespective of where the cue pointed.

Experiment 2

Experiment 2 had two aims. First, we sought to further corroborate the effect of an action-induced weighting of information in VWM observed in Experiment 1. Second, we investigated how spatially specific this effect is to the movement goal location. A set size of four (for which the effect was maximal in Experiment 1) was chosen, and the design was modified to allow for a systematic analysis of the impact of spatial distance between movement goal and test item. More specifically, we tested whether items that had been presented at locations neighbouring to the movement target location would also benefit from the higher degree of attentional engagement at that location, as compared to items that had been presented at non-neighbouring locations. To allow for the presentation of items spaced closely enough to be considered as neighbouring or non-neighbouring with a set size of four, the task was lateralized. In each trial, participants were to memorize four colours presented in one hemifield. The feature to be memorized was changed from orientation to colour in order to increase overall performance, which was rather low at the set size of four in Experiment 1. A second movement condition was included, in which participants were to point to the same goal location (the fixation dot) in each trial, irrespective of where the cue had pointed to.

Methods

Unless stated otherwise, the methods used in Experiment 2 were identical to those in Experiment 1.

Participants

Twenty students participated in the experiment. Data from five participants had to be excluded, one because performance did not exceed chance level and four because of the selfreported use of strategies that were likely to systematically affect performance (for example, always memorizing only the upper three items), as assessed by a questionnaire after the experiment. Analyses were performed on the remaining participants (10 female, 5 male, mean age = 23 years).

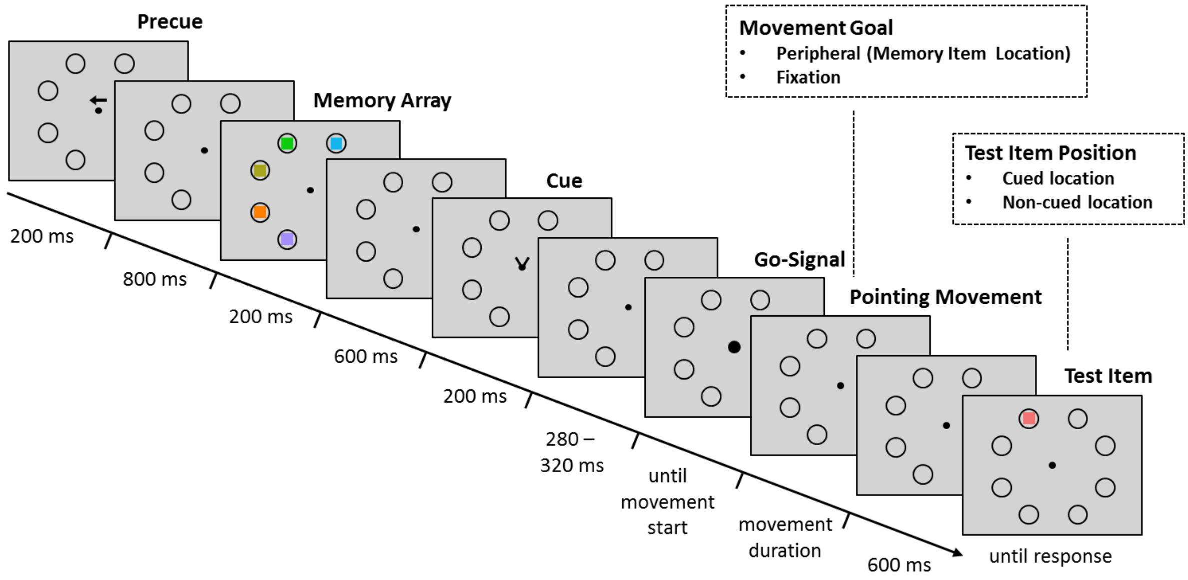

Figure 4. Trial procedure of Experiment 2. A trial started with an arrow (precue) presented above the fixation dot for 200 ms. This precue pointed to the left or right, thereby indicating the relevant visual hemifield for that trial. After 800 ms, the memory array was presented for 200 ms. Participants were instructed to memorize the colours of the four items in the hemifield indicated by the precue. After 600 ms, a cue was presented for 200 ms that symmetrically pointed to one of the four locations in each hemifield. Upon presentation of a goal-signal (enlargement of the fixation dot), presented after a variable delay of 280 – 320 ms, participants were to perform a pointing movement. In one half of the experiment, they were to point to the location indicated by the cue, in the other half of the experiment they were to point to the fixation dot. 600 ms after completion of the movement, a test item was presented at one of the locations until response. Participants were to indicate whether this test item was of the same colour as the memory item that had previously been presented at that location. In 25% of all trials, the test item was presented at the cued location, in 75% it was presented at one of the other three locations.

Procedure

The task is illustrated in Figure 4. Each trial started with the presentation of an arrow (precue) above the fixation dot for 200 ms, pointing to the left or right and thereby indicating the relevant hemifield for that trial. After an interval of 800 ms, the memory array was presented for 200 ms. It consisted of four coloured squares in each hemifield. Participants were instructed to memorize the colours of the squares in the hemifield indicated by the precue. After an interval of 600 ms, a spatial cue was presented for 200 ms. This cue was a line originating from the fixation dot, which pointed symmetrically to one of the four locations in each hemifield. To render the two hemifields physically identical, this line was mirrored along the vertical midline. After a short interval with a duration varying randomly between 280 and 320 ms, a go-signal in the form of an enlargement of the fixation dot was presented until the movement was initiated. In one half of the experiment, participants were then to perform a pointing movement to the location indicated by the cue, and in the other half they were to point to the fixation dot irrespective of where the cue had pointed. 600 ms after completion of the movement (i.e., after return to the start position), the test item was presented until response, and participants were to indicate whether or not there was a change in colour compared to the memory item that had previously been presented at that location.

Apparatus and Stimuli

The colour of each memory item was randomly selected from a set of seven isoluminant colours (blue, green, ocre, orange, pink, red, violet). All memory items within one hemifield had different colours. The colour of the test item was either identical to that of the memory item previously presented at that location or randomly selected from the remaining six colours.

Eight fixed locations served as memory item locations in the memory task and as targets in the movement task. These locations were arranged on an imaginary circle with a radius of approximately 4.68° of visual angle. Circle outlines (diameter 1.6° of visual angle) marked these locations and were present throughout the entire experiment. The memory items were 0.44° x 0.44° of visual angle in size, and the distance between memory items (centre to centre) was 3.31° of visual angle. The cue was a line (0.39° x 0.07° of visual angle) originating from the fixation dot. The fixation dot subtended 0.17° of visual angle.

Design

The main experiment consisted of 640 trials, organized in blocks of 32 trials each. Movement goal (peripheral vs. fixation) was changed after the first half of the experiment: In one half of the experiment, the movement goal corresponded to the location of a memory item indicated by the cue (peripheral goal), and in the other half the movement goal was the fixation dot. The order of these two movement goal conditions was balanced across participants. Test item position was varied on a trial-by-trial basis. All four memory item positions were equally likely to be tested, meaning that the test item was presented at the cued location in 25 % and at another location in 75 % of all trials.

Analyses of movement performance

As in Experiment 1, movement endpoints were determined using the recorded positional data, pointing errors and outliers were excluded from further analysis (on average, 3.5% of all trials), and the Index of Location Differentiation was calculated. In addition, movement onset and movement duration were compared for pointing towards fixation and pointing towards peripheral positions. This was done to ensure that the overall duration of the movements did not differ between movement conditions, seeing as this would systematically affect the duration of the maintenance interval and therefore most likely also performance. Movement onset was defined as the time from the onset of the cue until the onset of the movement (i.e., when the hand left the start position), and movement duration as the time from the start of the movement until return to the start position.

Analyses of memory performance

Trials with excessively long reaction times (> 2.5 SD from mean RT calculated separately for each participant; on average, 2.7% of all trials), pointing errors or pointing outliers were excluded from further analysis.

ANOVAs with the factors movement goal (peripheral vs. fixation) and test item position (cued location vs. non-cued location) were computed for accuracy in percent and mean reaction time. Trials in which test items were presented at non-cued locations were further split with respect to the distance to the cued location, that is, into trials in which the test item was presented at a location neighbouring or non-neighbouring to the cued location. Two-tailed t-tests (cued vs. neighbouring, cued vs. non-neighbouring and neighbouring vs. non-neighbouring) were computed separately for each type of movement goal (peripheral vs. fixation).

Results and Discussion

Similar to Experiment 1, the endpoints of the movements were well-clustered according to the different movement goals (Figure 2B shows the movement endpoints of a single participant) with a mean Index of Location Differentiation of 5.42 (SD: 1.75), ranging from 3.46 to 7.80. Timing parameters for movements towards peripheral memory item positions (movement onset: 443 ms ± 33 ms ; movement duration: 1891 ms ± 138 ms) and for movements towards fixation (movement onset: 470 ms ± 29 ms ; movement duration: 1918 ms ± 170 ms) did not differ significantly (movement onset: $t_{(14)} = 0.96$, $p = .355$; movement duration: $t_{(14)} = 0.35$, $p = .731$). Thus, the overall duration of the maintenance interval was the same in both pointing target conditions.

Figure 5A shows memory performance for the test items presented at the cued and at non-cued locations, separately for the two types of movement goal. Accuracy (Figure 5A, left panel) was highest ($F_{(1,14)} = 6.75$, $p = .021$, partial $\eta^2 = .33$) when the test item was presented at the cued location, as revealed by a main effect of test item position. Importantly, an interaction between movement goal and test item position ($F_{(1,14)} = 5.56$, $p = .033$, partial $\eta^2 = .28$) showed that the difference in accuracy for test items presented at cued and at non-cued locations was larger when the movement goal corresponded to the position of a memory item as compared to when the movement goal was the fixation dot. In fact, t-tests comparing accuracy for test items presented at the cued location against accuracy for test items presented at non-cued locations reached significance only when the movement goal was a peripheral memory item location, that is, when the test item position corresponded to the movement goal ($t_{(14)} = 3.17$, $p = .007$), but not when the movement goal was at fixation. Reaction times (Figure 5A, right panel) were shortest when the test item was presented at the cued location ($F_{(1,14)} = 11.39$, $p = .005$, partial $\eta^2 = .45$). The difference in performance for test items presented at cued and at non-cued locations was larger when the movement goal was the position of a memory item, although this pattern was less pronounced for reaction times than for accuracy, and the interaction fell just short of statistical significance ($F_{(1,14)} = 4.27$, $p = .058$, partial $\eta^2 = .23$). Reaction times were significantly shorter for test items presented at cued as compared to non-cued locations not only when the movement goal was a peripheral memory item position, that is, when the test item position corresponded to the movement goal ($t_{(14)} = 2.93$, $p = .011$), but also when the movement goal was the fixation dot ($t_{(14)} = 2.26$, $p = .04$).

To investigate the spatial specificity of the effect, trials in which test items were presented at non-cued locations were further split according to the distance to the cued location (Figure 5B). When the movement goal corresponded to the position of a memory item, performance was better for test items presented at the cued location as compared to items presented at neighbouring (reaction time: $t_{(14)} = -2.41$, $p = .03$) and non-neighbouring locations (accuracy: $t_{(14)} = 4.16$, $p = .001$; reaction time: $t_{(14)} = -3.34$, $p = .005$). Interestingly, performance at locations neighbouring to the cued location was still better than performance at non-neighbouring locations (accuracy: $t_{(14)} = 3.01$, $p = .009$; reaction time: $t_{(14)} = 2.34$, $p = .035$). When the movement goal was at fixation and did not correspond to the position of a memory item, performance was equivalent for all test item positions in terms of both accuracy and reaction time.

These results corroborate our finding of an action-induced weighting of information in VWM: Performance was better for memory items at locations that corresponded to the action goal than for items that had been presented at non-corresponding, action-irrelevant locations. Notably, this was the case even though the cue and therefore also the movement goal had no predictive value for the memory task, as all items were equally likely to be tested and thus equally relevant for the memory task. They only differed in their potential action relevance as indicated by the spatial correspondence between the memory item representation and the action goal. Indeed, when all memory items had been presented at action-irrelevant locations, that is, when the movement goal was the fixation dot, no difference in performance for items presented at cued and at non-cued locations was observed. Not only memory representations directly corresponding to action goals benefitted from the stronger attentional engagement at that location, but also representations of items presented at neighbouring locations. This suggests that there might be an attentional gradient within the spatial layout of VWM, with enhanced maintenance dropping gradually with increasing distance from the action goal location.

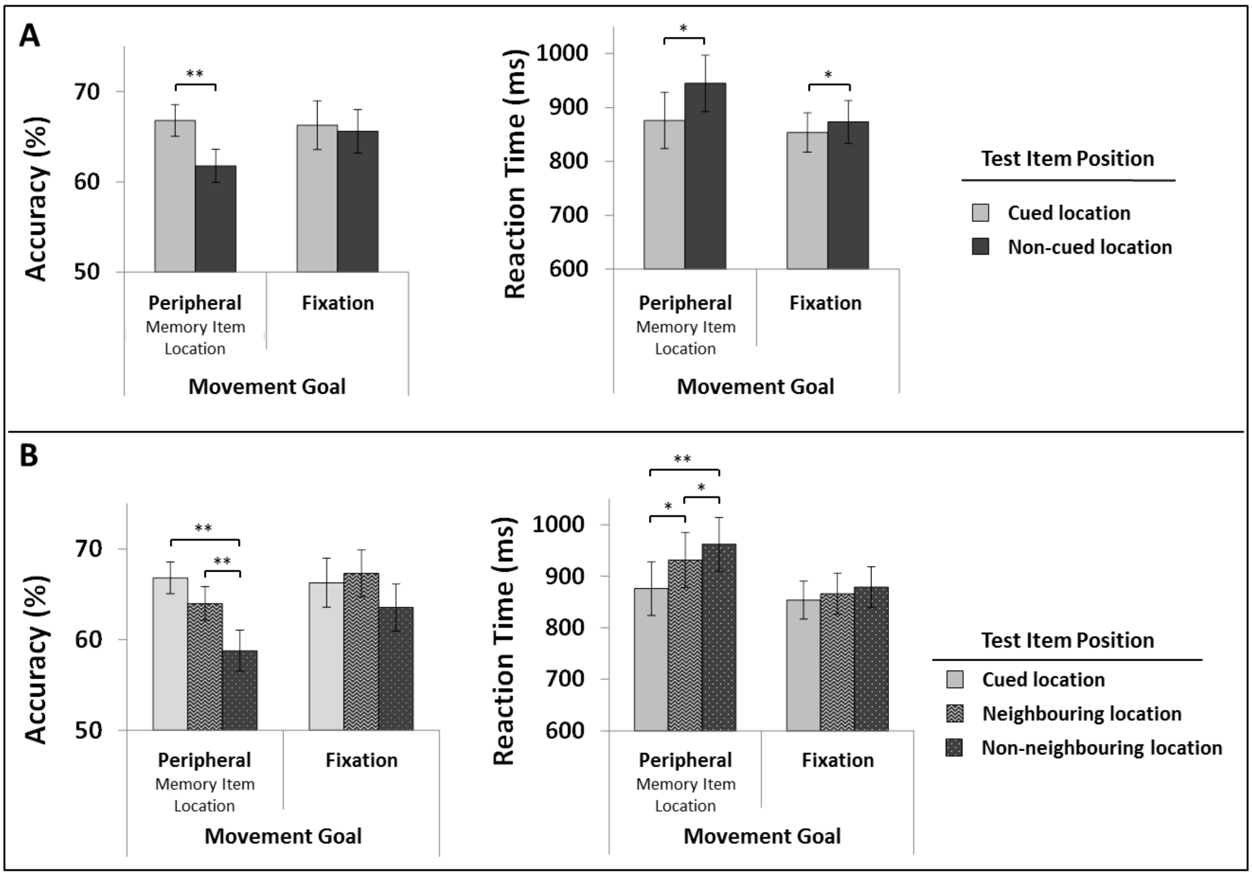

Figure 5. Results of Experiment 2. (A) Accuracy (left) and reaction time (right) shown separately for the two movement goal conditions (position of a memory item and fixation) and for test items presented at the cued (light grey) or at a non-cued location (dark grey). (B) Accuracy (left) and reaction time (right) shown separately for the two movement goal conditions (position of a memory item and fixation) and for test items presented at the cued location (light grey), and for non-cued locations that were either neighbouring (striped medium grey) or non-neighbouring (dotted dark grey) to the cued location. Asterisks mark significant differences (* p < .05; ** p < .01). Error bars show standard errors of the means.

General Discussion

The present experiments demonstrate that information in VWM is weighted according to its relevance for a current action goal: Performance for memory items that had been presented at movement goal locations was better than for items at action-irrelevant locations.

Notably, the movement goal was cued during the retention interval and well after the offset of the display containing the memory items. Therefore, this weighting cannot be explained by perceptual enhancement at movement goal locations prior to encoding, but was introduced at the representational level when the items were already being maintained. Neither can this weighting be attributed to a strategic allocation of visual selective attention to cued locations, because all items were equally likely to be tested in the memory task. The cue had no predictive value for the upcoming test item location, and the control conditions confirmed that the mere perception of the cue did not induce comparable differences in performance. Thus, the observed weighting of information can be attributed to differences between items in their potential action-relevance as indicated by a spatial correspondence between the retinotopic representation in VWM (Eimer & Kiss, 2010; Gratton, 1998) and the action goal. We propose that this effect was mediated by the automatic deployment of spatial attention to the action goal (e.g., Baldauf & Deubel, 2010) during item maintenance. Representations of items that had previously been presented at that location then benefitted from this stronger attentional engagement in a similar manner as when attention is explicitly deployed towards specific representations (e.g., Griffin & Nobre, 2003).

Experiment 1 also showed that this effect was sensitive to the number of items that were to be maintained, in that it was only observed for a set size at around average VWM capacity. It appears that when demand on the system is high and when it is accordingly likely that not all items can be successfully maintained, items that hold potential relevance for an action are prioritized. This sensitivity to memory load, however, may be related to the fact that all items were also and equally important for the memory task. When no other factors besides action intentions determine the relevance of visual information, a weighting may presumably be observed at smaller set sizes, or the action-irrelevant information would simply be excluded from further maintenance (Kuo et al., 2012; Williams et al., 2013; Zokaei et al., 2014).

Attentional enhancement of maintenance in VWM was not restricted to items that had been presented at the location of the action goal. Instead, the results of Experiment 2 suggest that there was an attentional gradient spreading out from the action goal location: Performance for items presented next to that location was slightly worse, but still better than for items presented at locations that were even further away. This finding contrasts with findings obtained for perceptual enhancement in perihand space. Tseng and Bridgeman (2011) tested whether placing one or two hands at the sides of the display would facilitate performance in such a graded fashion with performance dropping with increasing distance from the hand(s). They found no evidence of a gradient, but equally improved performance across the entire display. This finding was confirmed by another study investigating altered visual sensitivity in perihand space (Le Bigot & Grosjean, 2012). However, there are important differences between these studies and the present experiments that can account for these seemingly divergent findings. First, in these studies, one or both hands were continuously placed at the display throughout the experimental trials. Presumably, this highlighted the display itself as a potentially action-relevant object. When attention is directed to part of an object, so in this case to the parts of the display where the hands were placed, it typically spreads over the entire object (Abrams & Law, 2000; Egly, Driver, & Rafal, 1994; Moore, Yantis, & Vaughan, 1998). Thus, the uniform improvement of performance observed in these studies might be the result of object-based instead of spatial attention. Second, when we think of the functional implications in everyday life, it makes perfect sense that the mere presence of effectors near visual stimuli may have other effects on the allocation of attention than performing a pointing movement. Whereas the presence of an effector increases the general action affordance of objects in its vicinity, a pointing movement is usually performed to highlight very specific aspects of the environment. In a way, spatial specificity is the point of pointing. Interestingly, the abovementioned studies on altered visual processing in perihand space observed differential effects of placing the right, the left or both hands near the display for right- and left handers, which reflect the way they manually interact with their environment using their dominant and non-dominant hands (Le Bigot & Grosjean, 2012; Lloyd, Azañón, & Poliakoff, 2010; Tseng & Bridgeman, 2011). This indicates that typical functional implications do indeed influence the attentional engagement associated with different effectors and actions.

Correspondingly, a high spatial selectivity of attentional focussing has been observed for pointing movements. Baldauf et al. (2006) had participants perform a sequence of pointing movements and found an improvement of perceptual discrimination at the movement goal locations, but not at intermediate or other action-irrelevant locations (see also Baldauf & Deubel, 2009). Given that the locations were only 3.6° of visual angle apart, these results show that attentional selection was highly specific to the movement goals. Even though the distance between locations was about the same in our experiments (3.5° and 3.3°), we did not observe a similar specificity, but a graded improvement of performance. This may be related to the domain in which the stronger attentional engagement at the action goal took effect: Spatial specificity may be reduced when an action-related enhancement is introduced at the representational level in VWM as compared to at the perceptual level. Another possibility is that there was a similarly graded enhancement in the experiments of Baldauf et al. (2006), but that the enhancement at neighbouring locations was not strong enough to yield a benefit in performance in their highly demanding perceptual discrimination task. In comparison, the task of detecting a change in colour (Experiment 2) was relatively easy, and therefore even a weak attentional enhancement of spatially corresponding representations might have sufficed to result in improved performance.

To conclude, we have shown that differences in potential action-relevance induce a weighting of representations in VWM: memory performance for information that may be or become important for an action due to a spatial correspondence with the action goal is better than for information corresponding to action-irrelevant locations. Presumably, this action-induced weighting is mediated by the deployment of spatial attention to action goals. These findings demonstrate that our actions continue to influence visual processing beyond the perceptual stage, and extend our knowledge about how attentional processes optimize the efficient use of VWM by ensuring preferential maintenance of relevant information.

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Study V

Selective weighting of action-related feature dimensions in visual working memory

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Abstract

Planning an action primes feature dimensions that are relevant for that particular action, increasing the impact of these dimensions on perceptual processing. Here, we investigated whether action planning also affects the short-term maintenance of visual information. In a dual-task paradigm consisting of a memory and a movement task, participants were to memorize items defined by size or colour while preparing either a grasping or a pointing movement. Whereas size is a relevant feature-dimension for grasping, colour can be used to localize the goal object and guide a pointing movement. Results showed that memory for items defined by size was better during the preparation of a grasping movement than during the preparation of a pointing movement. Conversely, memory for colour tended to be better when a pointing movement was being planned than when a grasping action was being planned. This pattern was not only observed when the memory task was embedded within the preparation period of the movement, but also when the movement to be performed was only indicated during the retention interval of the memory task. These findings reveal that a weighting of information in visual working memory according to action-relevance can even be implemented at the representational level during maintenance, demonstrating that our actions continue to influence visual processing beyond the perceptual stage.

Introduction

Planning a goal-directed action involves a number of selection processes. For example, when our goal is to drink coffee from the mug sitting on the table in front of us, we need to select the appropriate action (reaching and grasping), effector (hand) and target (mug), and we need to extract the visual information that is required to specify movement parameters (e.g., location and size of the mug). It has been suggested that the latter is supported by an intentional weighting of task-relevant feature dimensions (e.g., size): Planning a particular action increases the impact of features coded on action-relevant dimensions, thereby ensuring that all the information necessary for online action control and the specification of open parameters is available (Hommel, 2009; Memelink & Hommel, 2013).

Indeed, actions have been shown to prime features of the goal object that are relevant for the respective action. Bekkering & Neggers (2002) asked participants to saccade to a target object presented among distractors, which was defined by a conjunction of orientation and colour, and then to either grasp the object or point to it. Orientation selection, as indicated by the accuracy of the first saccade, was better when the object was to be grasped than when it was to be pointed to. This selective enhancement has even been observed under rather unnatural conditions when two-dimensional images of objects had to be pointed to or grasped on a screen (Hannus, Cornelissen, Lindemann, & Bekkering, 2005).

A more general effect of action planning on selective visual processing has been demonstrated by studies that combined a movement task with an unrelated visual task. In a study by Fagioli, Hommel, & Schubotz (2007), participants had to detect a deviant in a temporal sequence of stimuli that predictably varied in size or location. When they were planning a grasping movement while monitoring the visual stimuli, the detection of size deviants was facilitated, whereas planning a pointing movement facilitated the detection of location deviants. Converging evidence has been obtained for selection in space: In a typical visual search task, detection of a target defined by size was facilitated during the preparation of a grasping movement, and detection of a target defined by luminance was facilitated during the preparation of a pointing movement although both tasks were unrelated and merely overlapped in time (Wykowska, Schubö, & Hommel, 2009). These studies show that planning a particular action does not only increase the weight of specific features of the goal object, improving goal selection, but the impact of an entire feature dimension on visual processing, modulating even early perceptual and attentional processes (see also Wykowska & Schubö, 2012).

The present study was motivated by the idea that the influence of action intentions on selective visual processing does not end at the perceptual stage. Whenever we want to make comparisons between objects separated in time or space, we need to retain the visual information about these objects over short periods of time, even if only for the duration of an eye movement. Consequently, visual working memory (VWM) forms a basis for a vast number of simple everyday tasks and for higher cognitive functions. It is, however, highly limited in its capacity (Luck & Vogel, 1997, 2013), necessitating selective processing to ensure that only relevant information takes up the available slots (or resources, see Ma, Husain, & Bays, 2014). Selective attention modulates VWM throughout all processing stages, from encoding up to retrieval (Gazzaley & Nobre, 2012), and there is accumulating evidence that information can be maintained in different representational states established by the allocation of attention, allowing for a weighting according to differences in task-relevance (Heuer & Schubö, 2016b; LaRocque, Lewis-Peacock, & Postle, 2014; van Moorselaar, Olivers, Theeuwes, Lamme, & Sligte, 2015). Experimentally, such a weighting is typically induced by cues presented during the retention interval that indicate some items as more behaviourally relevant than others based on their location or features (Gunseli, van Moorselaar, Meeter, & Olivers, 2015; Heuer & Schubö, 2016a).

In the present experiments, we investigated whether the planning of a particular action induces a selective weighting of items in VWM, resulting in better memory for items defined by a feature coded on an action-related dimension. In a dual-task paradigm, participants had to memorize items defined by colour or size while preparing a pointing or grasping movement. Whereas size is a critically relevant feature dimension for grasping movements (e.g., Smeets & Brenner, 1999), it should be of little or no relevance for planning a pointing movement towards the centre of an object. We therefore predicted better memory for size items when a grasping movement was to be performed than when a pointing movement was to be performed. Colour, in contrast, is not required for the specification of grasping parameters. Its relevance for pointing is not as apparent as that of size for grasping, but it might be used to localize the target object and guide the pointing movement in a similar manner as luminance (White, Kerzel, & Gegenfurtner, 2006). Accordingly, a second and more tentative hypothesis was that memory for colour items would be better while planning a pointing movement than during the preparation of a grasping movement.

Experiment 1 tested whether selective effects of action planning would become evident in memory performance by embedding the memory task within the action task (see Figure 1A, top row). While such effects would demonstrate that the preferential processing of action-related feature dimensions does have consequences for the short-term storage of visual information, they might be due to perceptual enhancement at encoding. To specifically test whether perceptual enhancement at encoding is determinant for actions to induce a selective weighting of information at the representational level in VWM, the cue indicating the movement to be performed was only presented during the retention interval in Experiment 2 (see Figure 1A, bottom row).

Methods

Participants

In total, fourty-nine students of Philipps-University Marburg participated in the experiments. Data from eight participants had to be excluded due to poor performance in the memory task (< 60% correct answers) or because they reported having used strategies not consistent with the instructions (e.g., focussing only on colour memory items) in a post-experimental questionnaire. Analyses were performed on the remaining participants (Experiment 1: 13 female, seven male, mean age 22 years; Experiment 2: 15 female, six male, mean age 24 years). All participants provided informed written consent, were naive to the purpose of the experiment, and had normal or corrected-to-normal visual acuity and colour vision. Visual acuity and colour vision were tested with the OCULUS Binoptometer 3 (OCULUS Optikgeräte GmbH, Wetzlar, Germany).

Apparatus

Participants were seated in a comfortable chair in a dimly lit room. On a table in front of them, a monitor was placed at a distance of approximately 104 cm from their eyes. At a distance of approximately 55 cm from the participants' eyes, a framed glass plate was mounted on the table. The glass plate was adjusted to the eye height of each participant to ensure that it always covered the entire monitor. Pointing and grasping movements were performed towards this glass plate. Participants had a wooden board with a response box to the left and a movement pad to the right in front of them. For the memory task, participants pressed the two buttons on the response box with their left middle and index fingers. The right hand was positioned on the movement pad, on which a cross marked the starting position for index finger and thumb. Stimuli were presented on a 22" screen (1680 x 1050 px). Stimulus presentation and response collection were controlled by a Windows PC using E-Prime 2.0 software (Psychology Software Tools, Inc.). Movements were recorded using a magnetic motion tracking device, and the experimenter sat approximately 2 m behind the participant to register whether the instructed movement (grasping or pointing) was executed.

Trial procedure and stimuli

The trial procedure is shown in Figure 1A. In Experiment 1, a trial started with the presentation of a movement cue for 200 ms, indicating the movement to be performed (see Figure 1B). Participants were instructed to prepare the shown movement, but to withhold movement execution. After an interval of 800 ms, the memory array was presented for 200 ms. This memory array consisted of ten circle-shaped items: four memory items and six distractor items. Two of the memory items deviated from the distractor items by their colour, and the other two by their size. Participants were instructed to memorize the colours and sizes of the deviating items. In

Experiment 2, the order of movement cue and memory array was reversed. After another interval of 900 (Experiment 1) or 800 ms (Experiment 2), a test item was presented at one of the memory item locations. The test item was always of the same dimension (size or colour) as the memory item that had previously been presented at that location, and participants were to indicate whether there was a change in size or colour (see Figure 1C). The response assignment was balanced across participants. The test item was present until response, but a quick reaction was encouraged. After the response, the test item disappeared for 200 ms. Upon its reappearance, participants were to execute the respective movement towards the glass plate in front of the monitor. For pointing movements, they were to point to the centre of the circle, touching the glass plate with the tip of their right index finger. For grasping movements, they were to perform a claw-like grasp (see Figure 1B), touching the glass plate with all five fingers along the outline of the circle. The next trial started 900 ms after return to the starting position.

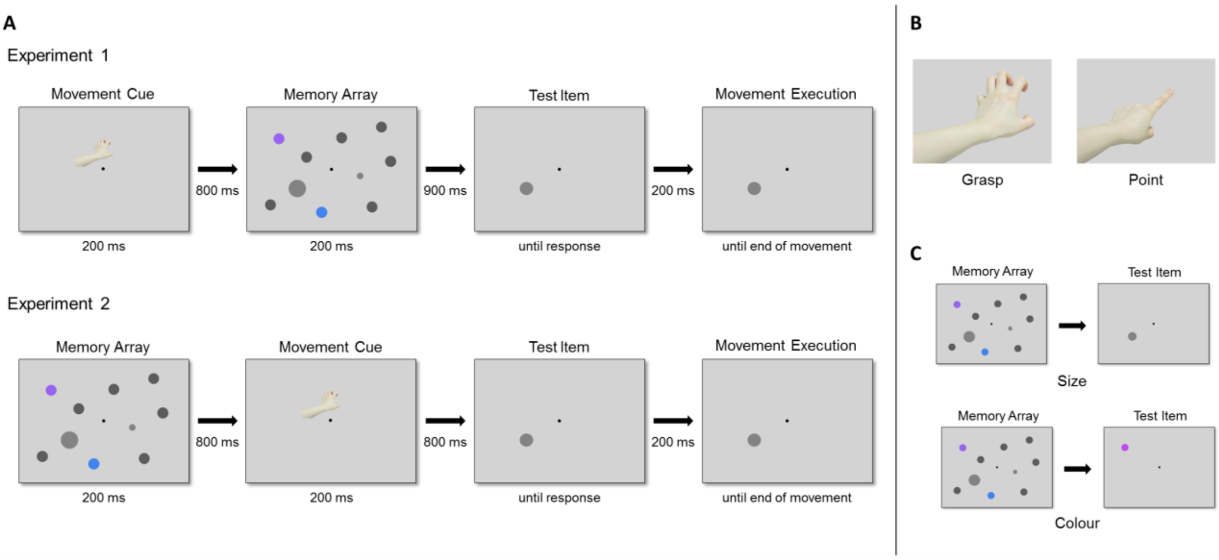

Figure 1. (A) Trial procedure in Experiment 1 (top row) and Experiment 2 (bottom row). In Experiment 1, a trial started with a movement cue indicating whether a pointing or grasping movement was to be planned. After 800 ms, the memory array was presented. The memory array consisted of ten items: four memory items and six distractor items. Two of the memory items deviated from the distractors by their colour, and the other two by their size. Participants were instructed to memorize the deviating items' colours and sizes. In Experiment 2, the order of movement cue and memory array was reversed. After an interval of 900 ms (Experiment 1) or 800 ms (Experiment 2) a test item was presented at one of the memory item locations. The test item was always of the same type (size or colour) as the memory item previously presented at that location. Participants were to indicate whether the test item was of the same or of a different colour / size as the corresponding memory item. After the response, the test item disappeared for 200 ms. Upon its reappearance, participants had to execute the respective movement towards the test item. (B) Movement cues for grasping (left) and pointing movements (right). (C) Examples of the memory task in a trial with a size test item (top row) and in a trial with a colour test item (bottom row).

All stimuli were presented against a grey background. The movement cues (see Figure 1B) were colour photos of a female volunteer's hand performing a grasping or pointing movement. They subtended an area of approximately 4.41° x 3.58° of visual angle. There were ten fixed item positions in the memory array, at eccentricities between 3.75 and 10.44° of visual angle from the fixation dot (0.17° of visual angle). Colour items and distractor items were 2.15° in diameter, and size items were 0.88°, 1.32°, 1.76°, 2.59°, 3.03° and 3.47° in diameter. The colours of the colour items were chosen from a set of six colours (green, turquoise, blue, slate blue, purple, magenta). For the two size memory items and for the two colour memory items, all combinations of different sizes and colours were equally likely. All memory items were isoluminant. The test item was always prominent in the same dimension (colour or size) as the memory item that had previously been presented at the respective location. In the 50% of trials with a change, colour test items had a colour that was spectrally neighbouring to the colour of the corresponding memory item, and size test items a size that was at least 0.88° and not more than 1.71° of visual angle different from the size of the corresponding memory item.

Design

There were four experimental conditions, as defined by the combinations of the factors test item type (size vs. colour) and movement type (grasping vs. pointing). Experimental condition was randomly chosen in each trial. All possible memory array configurations consisting of two colour items, two size items and six distractor items were equally probable. The experiment consisted of 560 trials, which were equally distributed among the four experimental conditions and organized in 14 blocks of 40 trials each.

Testing took place in two sessions on consecutive days. On the first day, participants performed short versions of the movement task and the memory task separately. The separate training tasks were identical to those in the dual-task paradigm of the main experiment and consisted of 160 trials each.. On the second day, they performed the main experiment and afterwards filled in a questionnaire to assess strategies and other factors that might have affected performance.

Data analyses

Trials with excessively long reaction times (> 2.5 SD from mean RT, calculated separately for each participant; on average, 2.6% of all trials in Experiment 1 and Experiment 2) and trials in which the wrong movement was performed (on average, 3.4% of all trials in Experiment 1 and 3.6% of all trials in Experiment 2) were excluded from further analysis. The primary measure of interest for memory performance with respect to the hypotheses was accuracy. Reaction times were analysed to ensure that speed-accuracy trade-offs did not contribute to any differences in accuracy. Accuracy in percent and mean reaction time were calculated separately for each movement and test item type. For reaction times, only trials with correct responses were included.

Results

Figure 2A shows performance in the memory task in both experiments, separately for the different movement and test item types. Two-way repeated measures ANOVAs with the factors movement type and test item type were computed for accuracy and reaction time. Of main interest was the interaction in terms of accuracy, indicating that memory for the two test item types differed between movement types. This interaction reached significance in both Experiment 1 ($F_{(1,19)} = 6.34$, $p = .021$, partial $\eta^2 = .25$) and Experiment 2 ($F_{(1,20)} = 7.07$, $p = .015$, partial $\eta^2 = .26$). No main effects were significant. In Experiment 1, there was also an interaction in reaction times ($F_{(1,19)} = 6.16$, $p = .023$, partial $\eta^2 = .25$), but no main effects. In Experiment 2, reaction times were faster in trials with pointing movements than in trials with grasping movements (F($_{1,20)} = 5.18$, $p = .034$, partial $\eta^2 = .21$), and faster for colour test items than for size test items ($F_{(1,20)} = 29.62$, $p < .001$, partial $\eta^2 = .60$).

To elucidate the observed interactions, specifically testing for a selective weighting of feature dimensions depending on the planned movement, performance in pointing trials was subtracted from performance in grasping trials, separately for size and colour test items (shown for accuracy in Figure 2B). For accuracy, positive values indicate better performance when a grasping movement was being planned, and negative values indicate better performance when a pointing movement was being planned. For reaction time, positive values indicate faster reaction times for pointing trials, and negative values indicate faster reaction times for grasping trials. These difference measures were tested against zero by means of one-tailed t-tests. Accuracy for size test items was significantly higher when a grasping movement was to be performed than when a pointing movement was to be performed, both in Experiment 1 ($t_{(19)} = 2.11$, $p = .024$) as well as in Experiment 2 ($t_{(20)} = 2.52$, $p = .01$). Accuracy for colour items tended to be higher during the preparation of a pointing movement, but this difference failed to reach significance (Experiment 1: $t_{(19)} = 1.32$, $p = .102$; Experiment 2: $t_{(20)} = .082$, $p = .211$). For reaction times, a significant positive value for size test items in Experiment 1 indicated slower responses during the planning of grasping movements than during the planning of pointing movements ($t_{(19)} = 2.23$, $p = .02$). None of the other comparisons for reaction times reached significance. To rule out that the effect in accuracy for size test items in Experiment 1 was due to a speed-accuracy trade-off, we calculated mean reaction time and accuracy for each quartile of the reaction time distribution, separately for each condition and participant. We then fitted orthogonal polynomials to accuracy as a function of reaction time. Across participants, there were significant negative linear coefficients that did not differ between conditions: in a two-way repeated measures ANOVA with the factors movement type and test item type, there were no main effects and no interaction, but the overall mean was significantly different from zero ($F_{(19)} =$

112.57, $p < .001$, partial $\eta^2 = .86$). Thus, there was no indication that higher levels of accuracy could be attributed to longer reaction times.

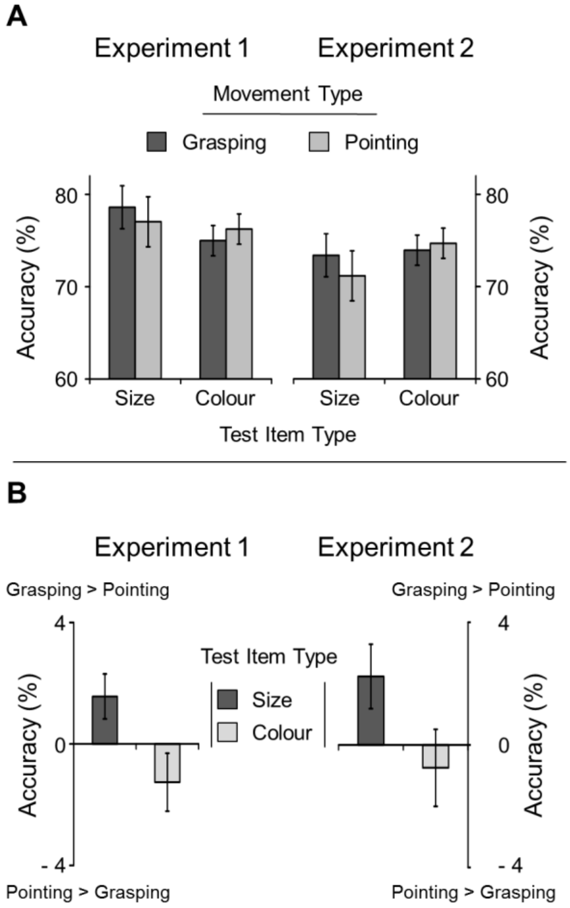

Figure 2. Results. (A) Accuracy in percent in Experiment 1 (left) and Experiment 2 (right), shown separately for the two test item types (size and colour) and for the two movement types (grasping in dark grey, pointing in light grey). (B) Differences in accuracy in grasping movement and pointing movement trials (grasping minus pointing) in Experiment 1 (left) and Experiment 2 (right), shown separately for size test items (dark grey) and colour test items (light grey). Positive values indicate better performance during the preparation of a grasping movement, and negative values indicate better performance during the preparation of a pointing movement. All error bars show the standard errors of the means.

Discussion

The present experiments show that the short-term storage of information in VWM is modulated by action intentions: memory for items defined by size was better when this feature dimensions was relevant for the action that was concurrently being prepared (i.e., a grasping action) compared to when it was irrelevant for the planned action (i.e., a pointing action). Conversely, memory for items defined by colour tended to be better during the preparation of pointing actions than during the preparation of grasping actions. However, this effect of action intention on memory performance for colour items did not reach statistical significance in either experiment. As outlined above, the action-relevance of colour for pointing actions is not very high and there are other studies that failed to find an effect of preparing a pointing action on performance (on perceptual performance in that case) for colour items (Bekkering & Neggers, 2002; Hannus et al., 2005). It might even be that the relevance of colour for pointing was particularly low in the present experiments due to the way the action goal object was presented: Colour can be used to guide pointing movements to the action goal (White et al., 2006), but here only one potential action goal was presented, rendering its localization and selection to guide the movement very simple.

Presumably, the effect of action intentions on maintenance in VWM is due to an intentional weighting of action-related feature dimensions, which has previously been established for visual perception (Memelink & Hommel, 2013). The results of Experiment 1 can be regarded as an extension of these findings. In Experiment 1, the memory task was embedded in the movement task, meaning that the movement was already being prepared when the to-be-memorized items were presented. One could accordingly interpret the observed effects of action intention on memory performance in Experiment 1 as the result of perceptual enhancement of action-related feature dimensions at encoding, demonstrating the consequences of action-related perceptual modulation on the short-term storage of visual information. The results of Experiment 2, by contrast, cannot be attributed to a modulation at the perceptual stage. Here, the movement to be performed was instructed during the retention interval and well after the presentation of the memory items. Thus, the observed differences in performance depending on current action intentions are likely due to a selective weighting of action-related feature dimensions in VWM introduced at the representational level during maintenance.

One could argue that the observed weighting of items arose during retrieval: In both experiments, participants were to respond to the memory task prior to executing the movement. The most likely mechanism to bring about improved performance for a specific feature dimension that would take effect at retrieval would be a prioritization, affecting the order of comparisons made between the items in memory and the displayed test item. In the present experiments, however, the number of required comparisons was already reduced to one by presenting only one test item at the previous location of the memory item it had to be compared to. More importantly, this test item determined the feature dimension that the comparison needed to be based on: it was either of a specific colour *or* of a specific size and thus only required comparisons within that dimension. A prioritization at retrieval therefore cannot account for the differences in performance for size and colour test items depending on action intention. A second mechanism that could be assumed to facilitate retrieval would be an enhancement of perception of the test item. However, given that the test item was perceptually not very demanding and presented until response, it is unlikely that this would affect performance. Moreover, any effect arising during retrieval, be it due to prioritization or perceptual enhancement, is likely to (also) reflect in reaction times and not only in accuracy as in the present experiments. Therefore, it is unlikely that the weighting of action-related feature-dimensions emerged during presentation of the test item.

In short, the present experiments show that the contents of VWM are selectively weighted according to the action-relevance of specific feature dimensions. Thus, action intentions modulate selective visual processing not only during early perceptual stages, but also during the short-term maintenance of visual information. These findings reveal a hitherto unknown mechanism of how the limited capacity of VWM is optimally used: action-related feature dimensions are enhanced, ensuring that the information that is needed for upcoming actions is easily available.

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Author contributions

Study I

Heuer, A. & Schubö, A. (2016). The focus of attention in visual working memory: Protection of focused representations and its individual variation. *PloS ONE, 11*, e0154228. doi:10.1371/journal.pone.0154228

AH and AS conceived and designed the experiments. AH collected and analyzed the data. AH and AS wrote the manuscript.

Study II

Heuer, A., & Schubö, A. (2016). Feature-based and spatial attentional selection in visual working memory. *Memory & Cognition, 44*, 621-632. doi: 10.3758/s13421-015-0584-5

AH and AS conceived and designed the experiments. AH collected and analyzed the data. AH and AS wrote the manuscript.

Study III

Heuer., A., Schubö, A., & Crawford, J.D. (submitted). Different cortical mechanisms for spatial vs. feature-based attentional selection in visual working memory.

AH, AS and JDC conceived and designed the experiments. AH collected and analyzed the data. AH, AS and JDC wrote the manuscript.

Study IV

Heuer., A., Crawford, J.D., & Schubö, A. (submitted). Weighting of information in visual working memory according to potential action-relevance.

AH and AS conceived and designed the experiments. AH collected and analyzed the data. AH, JDC and AS wrote the manuscript.

Study V

Heuer, A., & Schubö, A. (submitted). Selective weighting of action-related feature dimensions in visual working memory.

AH and AS conceived and designed the experiments. AH collected and analyzed the data. AH and AS wrote the manuscript.

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Zusammenfassung

Im visuellen Arbeitsgedächtnis kann Information über einen kurzen Zeitraum aufrechterhalten werden. Das ermöglicht beispielsweise den Vergleich von räumlich oder zeitlich getrennten Objekten, was für eine Vielzahl von Aufgaben benötigt wird. Die Kapazität des visuellen Arbeitsgedächtnisses ist jedoch nur sehr klein. Um sicherzustellen, dass diese begrenzte Kapazität effizient genutzt wird, bedarf es einer flexiblen Aktualisierung der Arbeitsgedächtnisinhalte, da sich die Relevanz visueller Information in der Interaktion mit unserer Umwelt permanent verändert. In den fünf Studien der vorliegenden Dissertation wurde diese Aktualisierung untersucht.

Der erste Teil der Dissertation (Studien I – III) widmete sich der Aktualisierung von Arbeitsgedächtnisinhalten in Folge von Hinweisreizen (Cues), die erst in der Behaltensphase dargeboten werden. Diese sogenannten Retrocues zeigen an, dass einige der Gedächtnisinhalte relevanter für die Gedächtnisaufgabe sind als andere. Das führt zu einer strategischen internalen Ausrichtung von Aufmerksamkeit und verbessert so die Gedächtnisleistung für diese Inhalte (z.B. Griffin & Nobre, 2003). Studie I zeigte, dass durch internale Aufmerksamkeitsausrichtung Inhalte im visuellen Arbeitsgedächtnis auch im Hinblick auf graduelle Unterschiede in ihrer Relevanz flexibel aktualisiert und gewichtet werden können. Die Gedächtnisleistung für die relevantesten und kontinuierlich attendierten Repräsentationen war verbessert, und dieser Leistungsgewinn hing mit der individuellen Effizienz attentionaler Kontrolle zusammen. Die Leistung für weniger aufgabenrelevante und zeitweise nicht attendierte Information war schlechter, aber deutlich über Zufallsniveau. Besonders wichtige Information wird somit im Fokus der Aufmerksamkeit in robuster Weise aufrechterhalten, während weniger wichtige Information in einem fragileren Zustand außerhalb dieses Fokus bereitgehalten werden kann.

Studien II und III demonstrierten die Flexibilität von Arbeitsgedächtnisaktualisierung hinsichtlich der genutzten visuellen Merkmale. Es zeigte sich, dass wirksame Retrocues unterschiedliche Merkmale der Gedächtnisinhalte betreffen können (direkt oder symbolisch angezeigte Position, Farbe oder Form). Die attentionale Auswahl von Repräsentationen kann somit auf unterschiedlichen visuellen Attributen basieren – je nachdem, welche Attribute Information über die Aufgabenrelevanz liefern. Rückgreifend auf Befunde zur Ausrichtung von Aufmerksamkeit auf visuelle Reize in der Außenwelt (Carrasco, 2011), konnten Studien II und II zudem zeigen, dass die Mechanismen räumlicher und merkmalsbezogener Aufmerksamkeit unterschiedlich sind. Studie II grenzte diese beiden Mechanismen auf der Verhaltensebene voneinander ab: merkmalsbezogene Retrocues (z.B. Farbe) ergaben Leistungsgewinne für Gedächtnisinhalte, die an benachbarten oder an nicht benachbarten Positionen dargeboten worden waren, wohingegen räumliche Retrocues die Leistung nur für solche Inhalte verbesserten, die an benachbarten Positionen dargeboten worden waren. Dies weist darauf hin, dass merkmalsbezogene Aufmerksamkeit im visuellen

Arbeitsgedächtnis global wirkt, und die Aufrechterhaltung relevanter Merkmale unabhängig von der räumlichen Konfiguration fördern kann. Räumliche Aufmerksamkeit hingegen wirkt lokal, und kann nicht gleichermaßen auf Repräsentationen von bei der Darbietung nicht räumlich benachbarter Reize zugreifen. Studie III untermauerte den Gedanken verschiedener Mechanismen für räumliche und merkmalsbezogene Auswahl durch eine doppelte Dissoziation auf kortikaler Ebene. Transkranielle Magnetstimulation des Gyrus supramarginalis verbesserte selektiv die räumliche Auswahl von Repräsentationen, wohingegen eine Stimulation des lateralen Okzipitalkortex selektiv die merkmalsbezogene Auswahl verbesserte. Da die gleichen Gehirnareale auch bei räumlicher und merkmalsbezogener Aufmerksamkeitsausrichtung auf perzeptuelle Ereignisse eine Rolle spielen (z.B. Murray & Wojciulik, 2004; Schenkluhn et al., 2008), deuten die Ergebnisse zudem darauf hin, dass die beiden Mechanismen selektiver Aufmerksamkeit auf Gedächtnis- und auf Wahrnehmungsebene überlappende neuronale Netzwerke involvieren.

Im zweiten Teil der Dissertation wurden die Effekte von natürlicheren Indikatoren der Relevanz bestimmter Aspekte unserer visuellen Umwelt untersucht: Handlungen und Handlungsintentionen. Statt Retrocues während der Aufrechterhaltung von Informationen im visuellen Arbeitsgedächtnis darzubieten, wurde in Studien IV und V eine Handlung als Zusatzaufgabe ausgeführt oder vorbereitet. Durch diese Handlung wurden bestimmte Arbeitsgedächtnisinhalte potentiell (handlungs-)relevanter als andere. Handlungen und Aufmerksamkeit sind eng miteinander verknüpft (z.B., Baldauf & Deubel, 2010), was den Gedanken nahelegt, dass die Vorbereitung einer bestimmten Handlung auch eine aufmerksamkeitsbasierte Arbeitsgedächtnisaktualisierung mit sich bringt, bei der Inhalte nach Unterschieden in der Handlungsrelevanz gewichtet werden. Die Untersuchung einer solchen handlungsinduzierten Aktualisierung orientierte sich hier an zwei Mechanismen selektiver handlungsbezogener Verarbeitung, die die visuelle Wahrnehmung beeinflussen: Die Ausrichtung von räumlicher Aufmerksamkeit auf ein Handlungsziel (z.B. Baldauf, Wolf, & Deubel, 2006; Study IV) und die stärkere Gewichtung handlungsrelevanter Merkmalsdimensionen (z.B. Memelink & Hommel, 2013; Study V).

Studie IV zeigte, dass Repräsentationen im visuellen Arbeitsgedächtnis auch dann bevorzugt aufrechterhalten werden, wenn sie räumlich mit einem Handlungsziel korrespondieren: Die Gedächtnisleistung für Inhalte, die an der Position eines Handlungsziels in einer für die Gedächtnisaufgabe im Prinzip irrelevanten Bewegungsaufgabe dargeboten worden waren, war besser als für die übrigen Inhalte. Dieser Effekt trat auf, wenn die Arbeitsgedächtnisbelastung an der durchschnittlichen Kapazitätsgrenze lag. Gedächtnisinhalte mit potentieller Bedeutsamkeit für eine Handlung werden folglich vor allem dann priorisiert, wenn die Beanspruchung des Gedächtnisses hoch ist. Der Einfluss handlungsbezogener Aufmerksamkeitsausrichtung auf die Aufrechterhaltung im visuellen Arbeitsgedächtnis war räumlich nicht auf die Position des Handlungsziels begrenzt, sondern nahm nur allmählich mit zunehmendem Abstand ab. Dieses Ergebnismuster deutet auf einen attentionalen Gradienten ausgehend von der Zielposition hin.

Studie V knüpfte an den Befund an, dass die Vorbereitung einer Handlung handlungsrelevante Merkmalsdimensionen bahnt und so ihren Einfluss bei der Wahrnehmung erhöht (z.B. Wykowska, Schubö & Hommel, 2009). Die Ergebnisse zeigten diesen Effekt von Handlungsintentionen auch bei der Aufrechterhaltung visueller Information: Die Gedächtnisleistung für Inhalte, die durch eine handlungsrelevante Merkmalsdimension definiert waren, war besser als für Inhalte, die durch eine handlungsirrelevante Merkmalsdimension definiert waren. Im Speziellen wurde beobachtet, dass die Gedächtnisleistung für Größe während der Vorbereitung einer Greifbewegung besser war als während der Vorbereitung einer Zeigebewegung, wohingegen das Erinnern von Farbe während der Vorbereitung einer Zeigebewegung besser war. Diese Gewichtung spiegelt die Handlungsrelevanz dieser Dimensionen wider. Während Größe relevant für Greifbewegungen ist, kann Farbe genutzt werden, um ein Ziel für eine Zeigebwegung zu lokalisieren.

Insgesamt zeigt die vorliegende Dissertation eine bemerkenswerte Flexibilität der Aktualisierung von Inhalten des visuellen Arbeitsgedächtnisses. Aufrechterhaltene Information kann unter Berücksichtigung gradueller Unterschiede ihrer Relevanz gewichtet werden (Studien I-V), sowohl wenn diese Relevanz explizit durch externale Cues definiert wird (Studien I-III) als auch wenn sie implizit eine Folge von Handlungsintentionen ist (Studien IV und V). Für die Auswahl relevanter Gedächtnisinhalte können verschiedene Repräsentationsmerkmale genutzt werden: Repräsentationen können wichtiger sein als andere, weil sie mit einer relevanten Position korrespondieren (Studien I-IV) oder weil sie ein Merkmal enthalten, das relevanter ist als andere Merkmale der gleichen Dimension (Studien II und III), oder das einer Merkmalsdimension angehört, die relevanter ist als andere Dimensionen (Studie V). Diese Flexibilität weist auf eine besondere Anpassungsfähigkeit des visuellen Arbeitsgedächtnisses hin, die eine effiziente Nutzung seiner stark begrenzten Kapazität angesichts eines Überschusses an visueller Information mit kontinuierlich variierender Relevanz möglich macht.

Curriculum Vitae und Publikationen

Die Seiten 159 – 161 enthalten persönliche Daten
und sind deshalb nicht Teil der Online-Veröffentlichung.

Erklärung

Hiermit versichere ich, dass ich die vorliegende Dissertation

"Flexible updating of visual working memory – The joint roles of attention and action"

selbstständig angefertigt habe. Ich habe mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient, und alle vollständig oder sinngemäß übernommenen Zitate als solche gekennzeichnet.
Die Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen anderen Prüfungszwecken gedient.

Marburg, Juli 2016

(Anna Heuer)